# BRACHIDIA OF LATE ORDOVICIAN AND SILURIAN EOSPIRIFERINES (BRACHIOPODA) AND THE ORIGIN OF THE SPIRIFERIDES

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ABSTRACT. The brachidium is revealed for the first time in the Late Ordovician *Eospirifer praecursor*, the earliest known eospiriferine and probably the ancestor of the entire *Spirifer* group. The adult stages of the species possess a spiralium directed ventro-laterally with a pair of small jugal processes without a jugum. The brachidium of the other five species of *Eospirifer* (including *E. radiatus* (Sowerby), the type species) and three of *Striispirifer* (including *S. plicatellus* (Linnaeus)) from the Llandovery, Wenlock or Ludlow in South China, Kazakhstan, England, Sweden and Canada are also revealed and reconstructed, demonstrating the same type of brachidium as in *E. praecursor*. The structure of the early brachidial growth stage of *E. praecursor* is similar to that of the adult stages of the early atrypoid *Cyclospira bisulcata* (Emmons). This, coupled with the evidence of cardinalia, is of significance in the evaluation of cospiriferine origins. A shallow-water environment is proposed for the origination of the Spiriferida. *Eospirifer*, a progenitor and Lazarus genus, probably originated in East and Central Asia in the mid Ashgill; it disappeared in the late Ashgill, but survived the latest Ordovician mass extinction, recovered in Asia and Australia in the Early–Mid Llandovery, and did not spread to Europe and America until the later Llandovery (about the *sedgwickii* Biozone). A striated cardinal process is also seen for the first time in the topotype of *E. radiatus*, indicating that its presence may not be of fundamental significance in the generic classification of the eospiriferine group.

RECENTLY Rong *et al.* (1994) described the oldest known eospiriferine species, *Eospirifer praecursor*, from the Upper Ordovician (middle Ashgill) Changwu Formation, Pengli, Jiangshan, south-western Zhejiang Province, East China (Text-fig. 1). It is the first reliable record of the eospiriferines in the Ordovician and it verifies that the eospiriferines, the earliest representatives of the *Spirifer* group, made their first known appearance in the mid Ashgill, Late Ordovician. It was not possible, however, to make serial sections to reveal the brachidium of *E. praecursor* since the material studied and figured in 1994 is composed only of external and internal moulds of both valves (collected by the present authors during their first field excursions to the area in 1991).

A large quantity (nearly 5000 individuals) of conjoined valves of *E. praecursor* was gathered from three bedding planes of calcareous mudstone in the Xiazhen Formation, Zhuzhai, 15 km south-east of Yushan County Town, north-eastern Jiangxi Province, East China (Text-fig. 1) by Zhan Ren-bin and Fu Li-pu in 1992, and by the present authors in 1994. Within the Xiazhen Formation occur other genera of brachiopods (such as *Tcherskidium*, *Altaethyrella*, *Kassinella*) and corals (*Agetolites*), suggestive of a mid Ashgill age for this formation (Text-fig. 2). Discoveries of conjoined valves have now made serial sectioning possible. More than 30 specimens of this species have been sectioned systematically to reveal the internal morphology of ventral and dorsal valves in a state of good preservation. The purpose of this paper is to show the internal structures of *E. praecursor*, in particular the brachidium. Comparisons of the brachidium of the Late Ordovician *E. praecursor* with Silurian (Llandovery, Wenlock and Ludlow) eospiriferines from South China, Kazakhstan, England, Sweden, and East Canada (Text-fig. 3; Appendix) are also made in this paper. These include some species of *Eospirifer* Schuchert, 1913 and *Striispirifer* Cooper and Muir-Wood, 1951 with *Hedeina* Boucot, 1963 (subjective synonym of *Striispirifer*; see
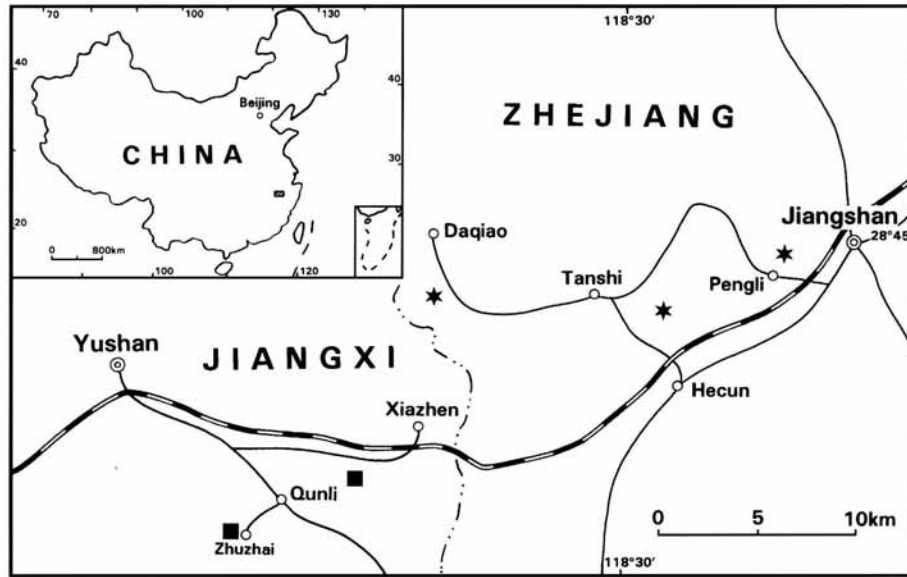
TEXT-FIG. 1. Location of the study area where *Eospirifer praecursor* was collected. Stars indicate localities yielding specimens preserved as moulds; squares localities with conjoined values.
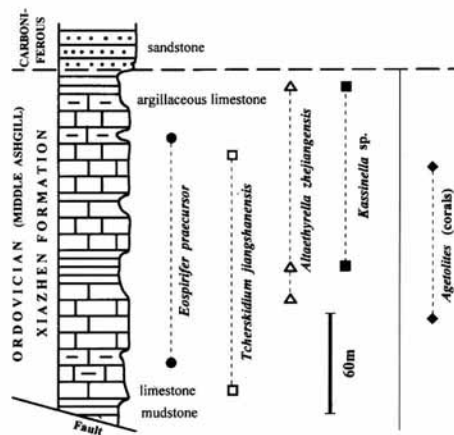
TEXT-FIG. 2. Stratigraphical distribution of *Eospirifer praecursor* along with other main taxa at the Zhuzhai section, Yushan, north-eastern Jiangxi Province, East China.

Bassett and Cocks 1974). The origin of the eospiriferines is further discussed based on new data from comparisons of the brachidia of the earliest known eospiriferines with some related groups.

The brachidium of the eospiriferines was often neglected by palaeontologists when they studied this group and their external morphology has become the most important basis for their classification. Discoveries of a pair of small jugal processes in *E. praecursor* and *E. radiatus*

TEXT-FIG. 3. Stratigraphical range of species assigned to *Eospirifer* and *Striispirifer* studied in this paper.

SYSTEM	SERIES		*Eospirifer*	*Striispirifer*
S I L U R I A N	PRIDOLI			■ *yunnanensis*
	LUDLOW			
	WENLOCK		● *radiatus* ● (Gotland) (England)	■ *plicatellus*
	LLANDOVERY	Telychian	● cf. *radiatus*	
		Aeronian	● *songkanensis* ● *minutus*	■ *acuminiplicatus*
		Rhuddanian	● *sinensis* ● *cinghizicus*	
ORDOVI-CIAN	ASHGILL	Late Middle Early	● *praecursor*	

(Sowerby) examined in this paper, support an observation made by Boucot (1963) but are not in accordance with that given by St Joseph (1935) who illustrated a band between two primary lamellae of the spiralia in *E. radiatus* (p. 322, text-fig. 3). Discussions on the real nature of the brachidia in different species of eospiriferines will be given below. The internal morphology of nine taxa of eospiriferines (see Appendix) is revealed in terms of the technique of serial sections using rapid-drying, acetate peels and a camera-lucida microscope (Wild Heerbrugg). A dorsal three-dimensional view of the brachidium of the dorsal valve in eospiriferine species has been reconstructed by tracking various points of different positions of the structures from transverse section planes into longitudinal, commissure planes. The lateral views of the brachidial reconstructions have also been produced by the same method, but normally only the right spiralium, as viewed into the dorsal valve, has been drawn.

NEW OBSERVATIONS ON *EOSPIRIFER PRAECURSOR*

More than 30 specimens of the Ashgill *E. praecursor* Rong, Zhan and Han, 1994 have been sectioned, and selected serial transverse sections of two specimens of conjoined valves are illustrated in this paper. Text-figure 4A–B illustrates a larger adult shell (6·45 mm wide) and one of the smallest young shells (2·9 mm wide). Brachidia of the two specimens are reconstructed in Text-figure 5A–B. New observations are made on the crura, primary lamellae, spiralia and jugal processes in the following section.

Crura and primary lamellae. The plates supporting crural bases are basically lacking and thus the crura are located freely posteriorly; the crura and primary lamellae are slightly divergent (30–40°), adjacent to the dorsal valve, extending near the anterior commissure, and afterwards turn and curve ventrally and then posteriorly to form spiralia.

In the early stages (Text-figs 4A, 5A), crura are rod-like posteriorly; central inclination is not prominent. Starting from a position close to the junction of the crura and primary lamellae, the crura become plate-like, noticeably concave ventrally, and are moderately inclined internally, with an angle of 80° at the point of transition, where the primary lamellae are less inclined internally (40°, becoming subparallel anteriorly).

In the adult stages (Text-figs 4B, 5B), crura are rod-like posteriorly and then plate-like near the junction of the crura and primary lamellae, slightly concave ventrally at their lateral ends, and strongly inclined centrally, with an angle of about 110°; afterwards the crura are prolonged anterior to the primary lamellae of the spiralia, and the thin, plate-like primary lamellae are posteriorly more
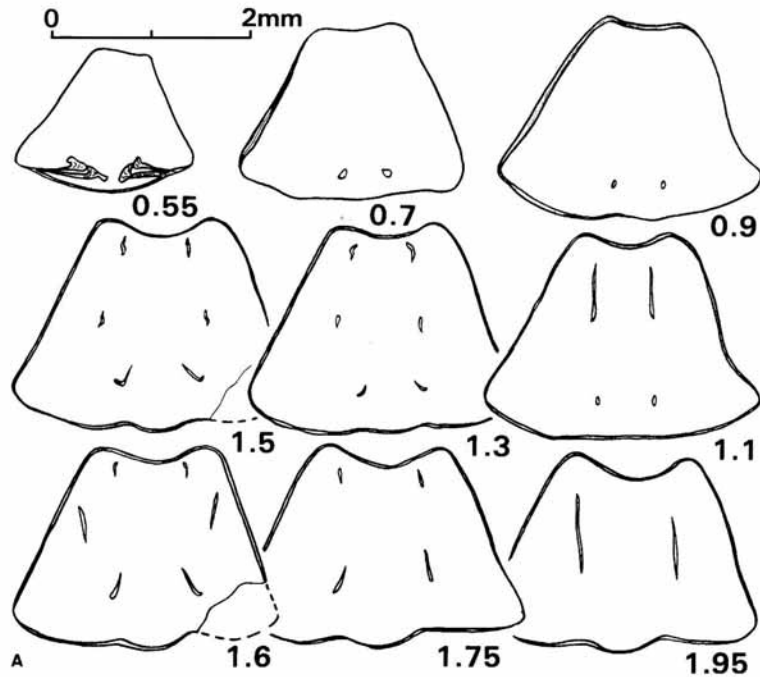
TEXT-FIG. 4A. For caption see facing page.

strongly inclined internally, with an angle of 120–130°, and then turn to be less inclined internally, with an angle of 110–100° anteriorly.

Spiralium and jugal process. The most important and significant discoveries are the lophophore supports (brachidium) which have to date not been described in the early eospiriferines (Ashgill to early Mid Llandovery). Our new discoveries demonstrate that the brachidium of *E. praecursor* in adult stages is essentially the same as that of the Silurian eospiriferines examined by Boucot (1963) and the present authors. The brachidium is characterized by the following features: (1) continuous calcite growth from crura to spiralia with the junction between them commonly smooth and not sharply geniculate; (2) a spiralium consisting of only one-and-one-half whorls in very small individuals (Text-fig. 5A) and of three to four whorls in adult specimens (Text-fig. 5B), the axis of the spires being directed laterally in early stages and ventro-laterally in adult stages; the spires lying as a whole nearer the ventral valve; the first whorl almost touching the inner walls of the ventral valve; the spires in the early stages located outside the primary lamellae and in the adult stages located not only outside but within the space between the divergent primary lamellae; (3) a pair of very small, separated jugal processes acuminated centro-ventrally in the adult, but not seen in very small individuals (less than 3·0 mm wide); (4) the lack of any kind of jugum.

BRACHIDIUM OF OTHER EARLY EOSPIRIFERINES

Serial transverse sections of topotype specimens of some species of *Eospirifer* have been made (see Appendix), including: (1) *Eospirifer cinghizicus* Borisiak (Early Llandovery); (2) *E. sinensis* Rong,
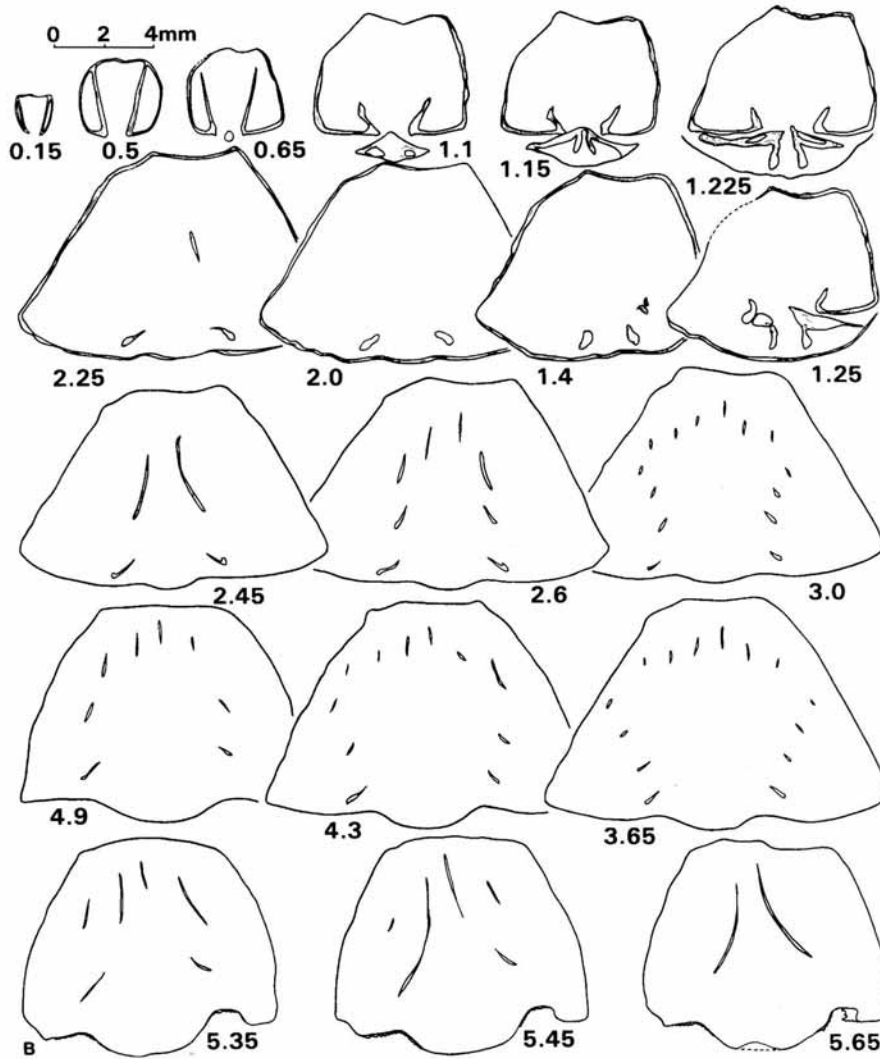
TEXT-FIG. 4A–B, serial transverse sections of two specimens of *Eospirifer praecursor* Rong, Zhan and Han, 1994. Xiazhen Formation (middle Ashgill), Zhuzhai, Yushan. A, for the smaller specimen (length 3·1 mm, width 2·9 mm, depth 2·2 mm), NIGP 124766 (10 sections made and 9 selected herein). B, for the larger specimen (length 6·5 mm, width 6·45 mm, depth 4·45 mm), NIGP 124767 (57 sections made and 19 selected herein).

Xu and Yang (late Rhuddanian, Early Llandovery); (3) *E. minutus* Rong and Yang (early Aeronian, Mid Llandovery); (4) *E. songkanensis* Wu (late Aeronian, Mid Llandovery); (5) *E.* cf. *radiatus* (Sowerby) (Late Landovery) and (6) *E. radiatus* (Sowerby) (Late Wenlock; both British and
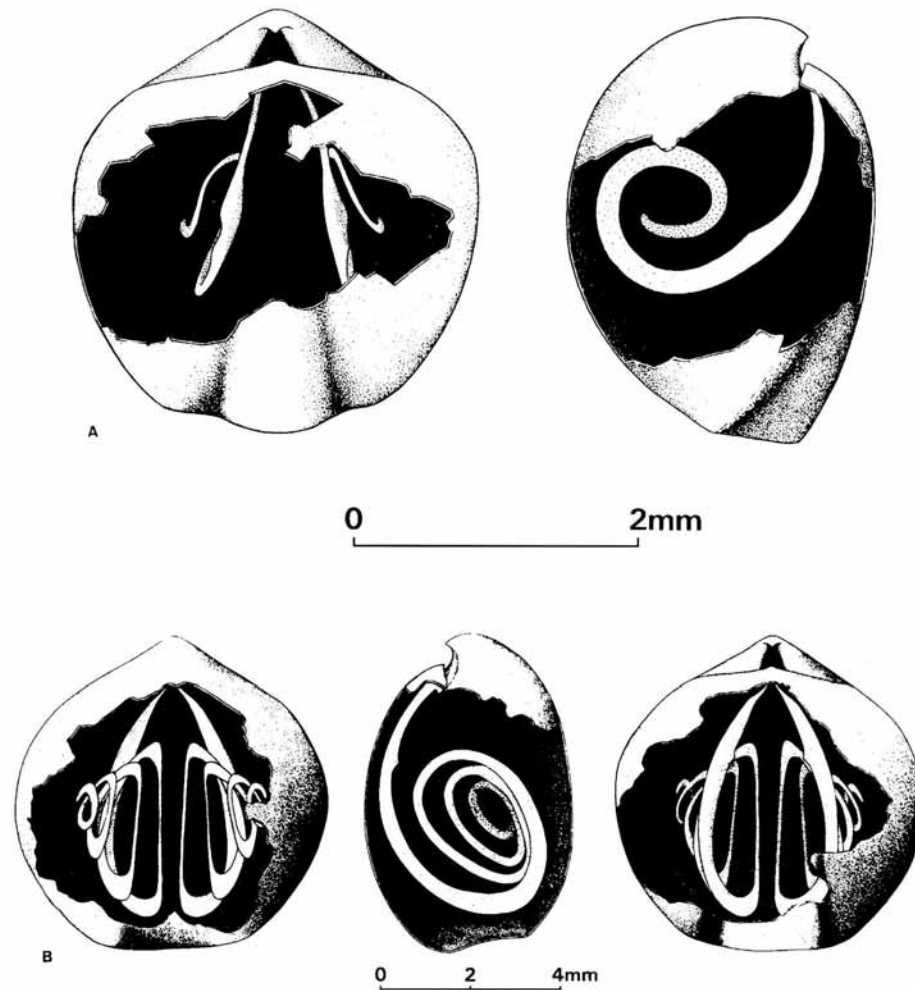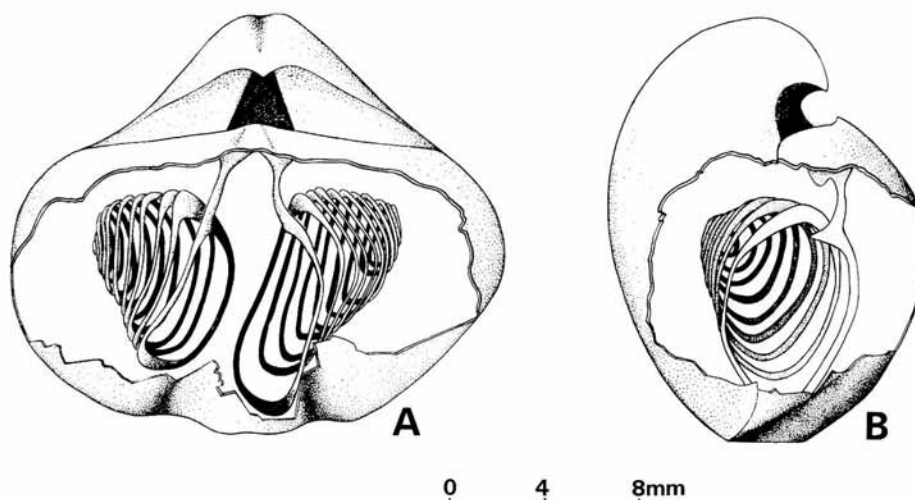
TEXT-FIG. 5A–B, reconstruction of brachidia of two specimens of *Eospirifer praecursor* Rong, Zhan and Han, 1994 based on Text-figure 4A–B respectively. Note the simple spiralium in the smaller specimen (A; lateral view shows only one-and-one-half whorls).

Swedish specimens). Reconstructions of all their brachidia, except for those of *E. cinghizicus* and *E. songkanensis*, are made based on these sections. New investigations reveal that the brachidium of the Llandovery and Wenlock taxa of *Eospirifer* is of the same type as that of Late Ordovician *E. praecursor*.

TEXT-FIG. 6. Serial transverse sections of one specimen of *Eospirifer sinensis* Rong, Xu and Yang, 1974 (length 16·6 mm, width 19·9 mm, depth 11·7 mm); NIGP 124768 (65 sections made and 19 selected herein); Lower Xiangshuyuan Formation (upper Rhuddanian), Leijiatun, Shiqian, north-eastern Guizhou, South-west China.
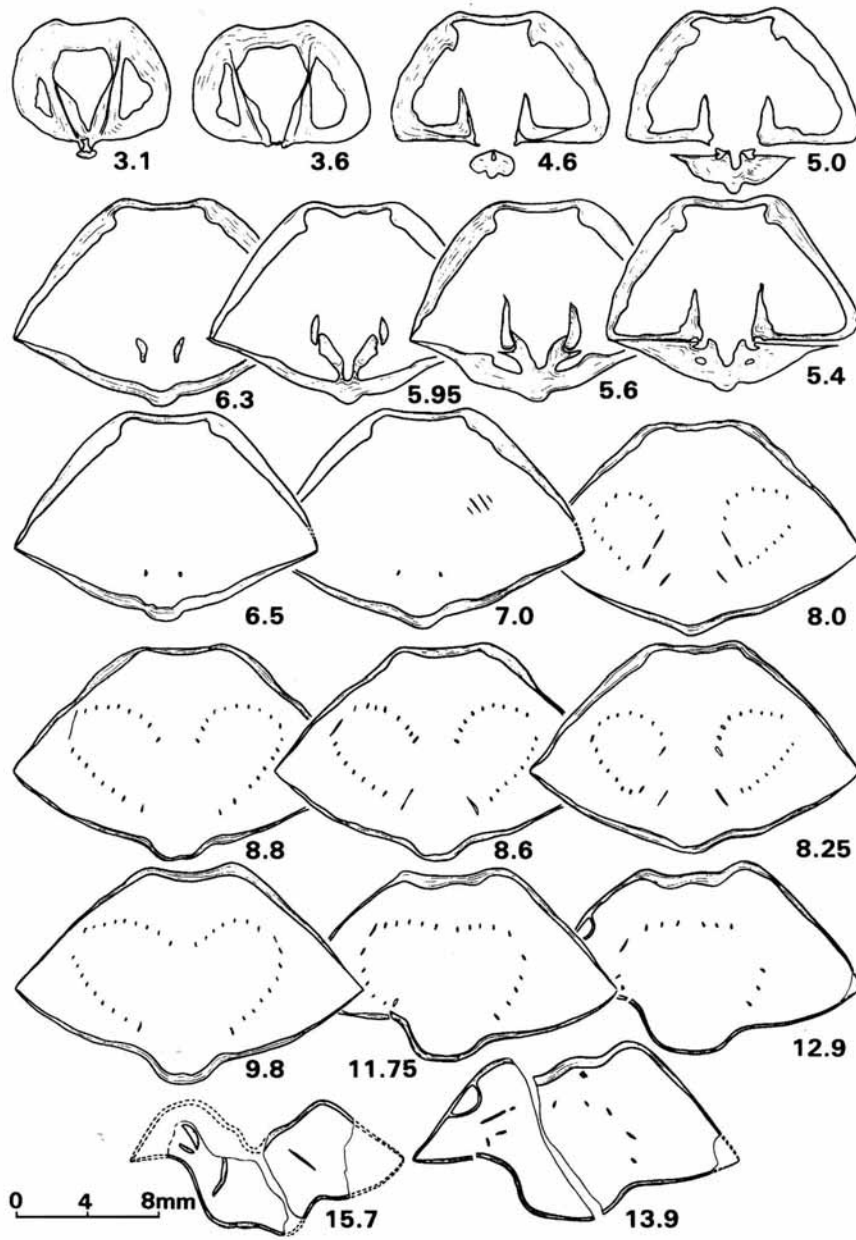
TEXT-FIG. 6. For caption see opposite.

TEXT-FIG. 7. Reconstruction of brachidia of one specimen of *Eospirifer sinensis* Rong, Xu and Yang, 1974 based on Text-figure 6.

Topotype specimens of *E. sinensis* have been transversely sectioned in detail. The good preservation of the material has made it possible to reveal their internal structures as shown in Text-figures 6–7. There are no substantial differences between the brachidia of *E. sinensis* and *E. praecursor*. The number of spiralial whorls in the adult stages of *E. sinensis* and *E. praecursor* is eight to nine and three to four respectively, mainly due to the difference in shell size.

The brachidia of the early Aeronian *E. minutus* and the late Aeronian *E. songkanensis* (see Appendix) are also the same as that of the earliest taxon of the same group (for *E. minutus*, see Text-figs 8–9). All species examined herein have short but prominent jugal processes with the exceptions of *E. minutus* (8–10·5 mm wide, 7–10 mm long, and 6–8·5 mm thick), *E. songkanensis* (22·0 mm wide, 19·3 mm long, and 14·0 mm thick), and the juvenile specimen of *E. praecursor* (3·1 mm long, 2·9 mm wide and 2·2 mm thick). This is not because shell size is too small to develop the processes. The adult stages of *E. praecursor* have even smaller shells (usually only 4–5 mm, occasionally 6 mm wide) than those of *E. minutus* and *E. songkanensis* but still has well established jugal processes. Thus, features of the jugal processes may be of fundamental significance in specific classification.

A topotype specimen of *E. cinghizicus* Borisiak (see Appendix), from the Lower Llandovery of

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EXPLANATION OF PLATE 1

Figs 1–17. *Eospirifer praecursor* Rong, Zhan and Han, 1994. 1–12, 17, Xiazhen Formation (middle Ashgill); Zhuzhai, Yushan, north-eastern Jiangxi, East China; 1–2, 9, 17, NIGP 124755. 1, 9, ventral and lateral views of conjoined valves; ×8; 2, 17, dorsal view of the valves; ×8, ×20 (local enlargement showing fine radial striae). 3–7, NIGP 124756; anterior, posterior, ventral, dorsal and lateral views of conjoined valves; ×8. 8, 10–12, NIGP 124757; anterior, posterior, dorsal and ventral views of conjoined valves; ×8. 13–16, NIGP 118704, holotype; Changwu Formation (Middle Ashgill); Pengli, Jiangshan, south-western Zhejiang, East China; 13–14, fine radial striae; ×20; 15, detailed view of cardinalia; ×30; 16, internal mould of dorsal valve; ×10.

PLATE 1
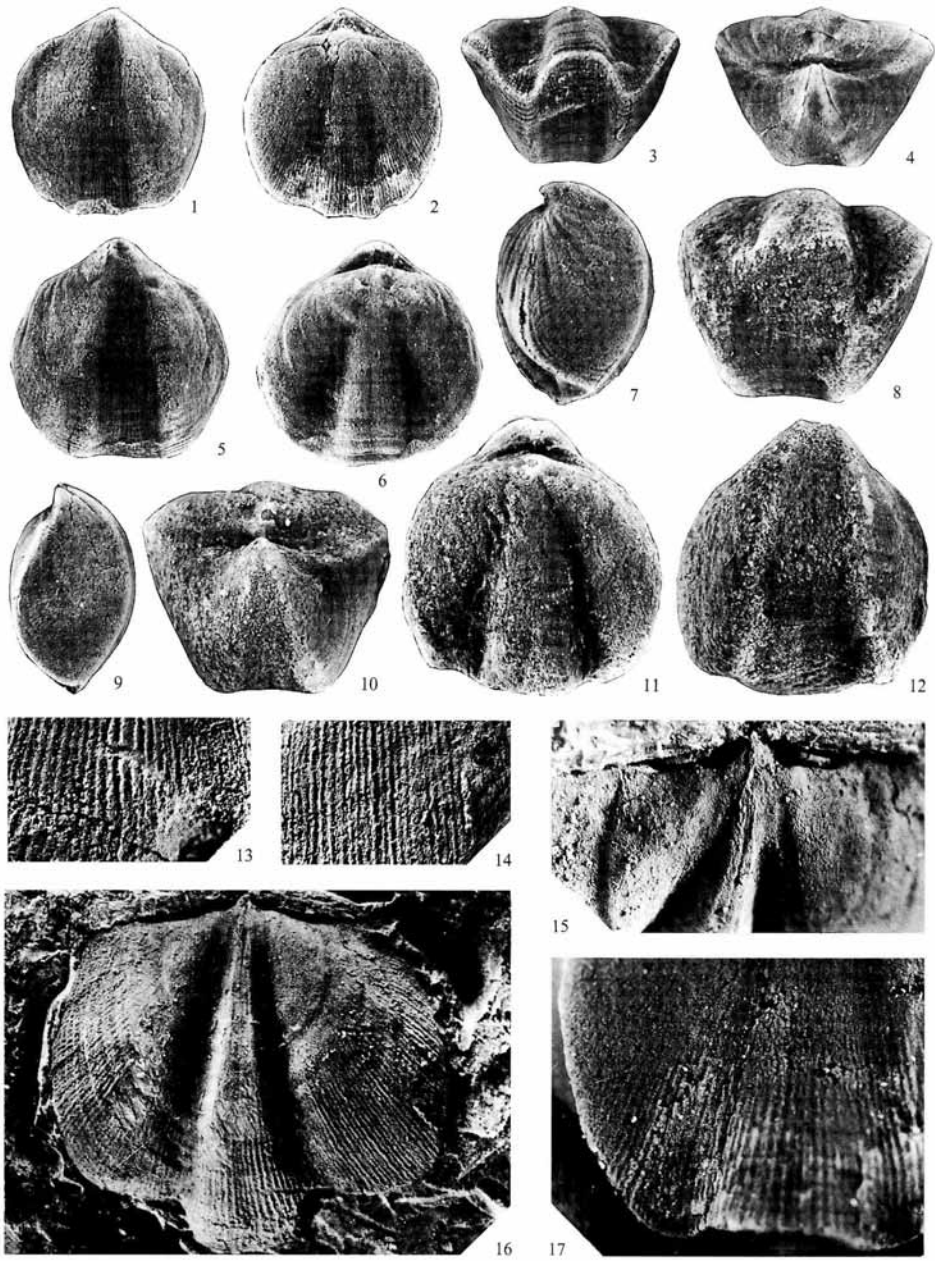
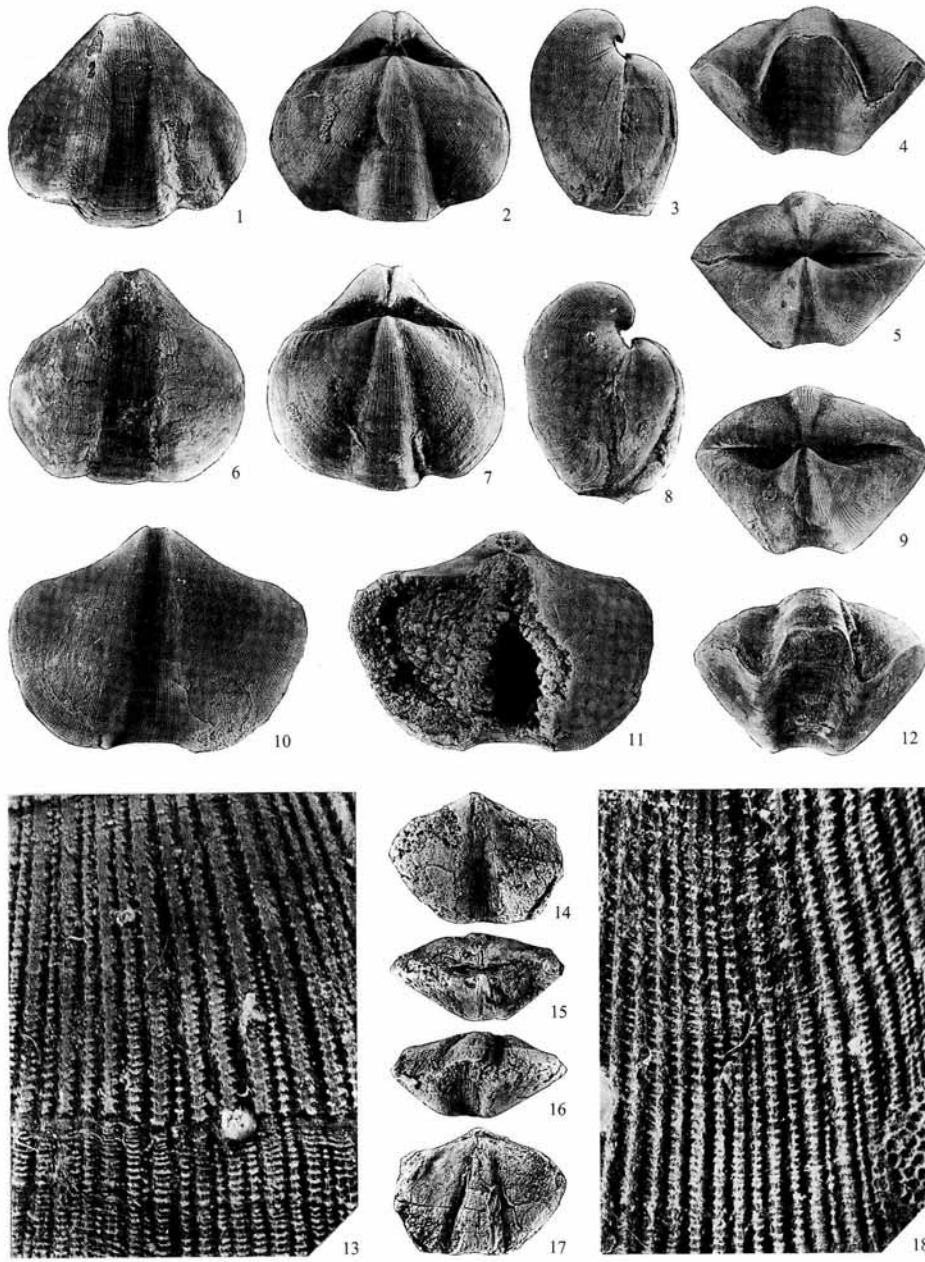RONG and ZHAN, *Eospirifer praecursor*
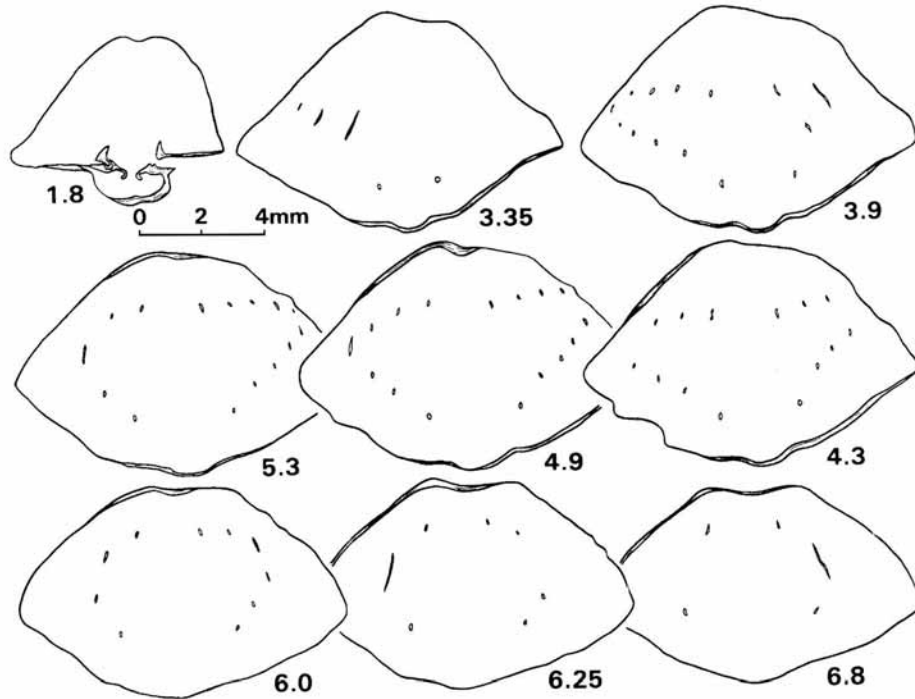
TEXT-FIG. 8. Serial transverse sections of one specimen of *Eospirifer minutus* Rong and Yang, 1978 (length 9·7 mm, width 11·0 mm, depth 7·4 mm); NIGP 124769 (21 sections made and 9 selected herein); Middle Xiangshuyuan Formation (lower Aeronian), Yingwuxi, Sinan, north-eastern Guizhou, South-west China.

Chinghiz, Kazakhstan, was sectioned, but unfortunately no spiralium was detected because the preservation is inadequate. Nevertheless, a pair of small jugal processes can be observed from the serial sections (Text-fig. 10). This species is characterized by a thick secondary shell having solid or very small apical cavities posteriorly in both valves, crural bases close to each other, and the two primary lamellae almost parallel.

Figs 1–9, 12. *Eospirifer sinensis* Rong, Xu and Yang, 1974; Xiangshuyuan Formation (upper Rhuddanian, Lower Llandovery); Leijiatun, Shiqian, north-eastern Guizhou, South-West China, 1–5, NIGP 45215, topotype; ventral, dorsal, lateral, anterior and posterior views of conjoined valves; ×2. 6–9, 12, NIGP 22302, holotype; ventral, dorsal, lateral, posterior and anterior views of conjoined valves; ×2.

Figs 10–11. *Eospirifer* cf. *radiatus* (Sowerby); NIGP 124758; Jupiter Formation (C650) (Telychian, Upper Llandovery); Anticosti, Canada; ventral and dorsal views of conjoined valves (on the specimen in fig. 11 most of the dorsal shell is broken, showing the spiralium); ×1·5.

Figs 13, 18. *Eospirifer radiatus* (Sowerby, 1834); NIGP 124759; Mulde Beds (SW16) (middle–upper Wenlock), Gotland, Sweden; detailed views of fine radial striae with concentric filae on a ventral valve (see Pl. 3, fig. 14); ×15.

Figs 14–17. *Eospirifer cinghizicus* Borisiak, 1955; NIGP 124760; *Cinghizicus* Bed of Al'peisskii Horizon (Llandovery), Chinghiz, Kazakhstan; ventral, posterior, anterior and dorsal views of conjoined valves; ×2.

PLATE 2

RONG and ZHAN, *Eospirifer*
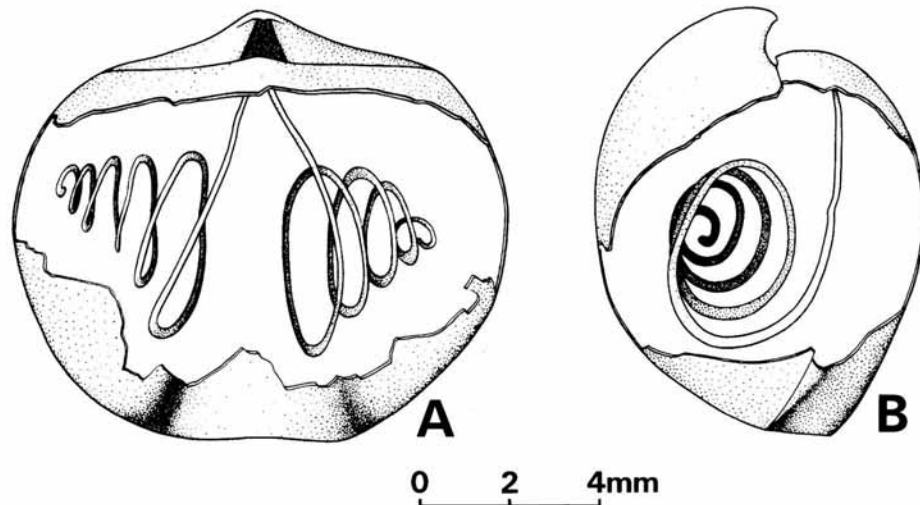
TEXT-FIG. 9. Reconstructions of brachidia of one specimen of *Eospirifer minutus* Rong and Yang, 1978; based on Text-figure 8.

The brachidium of *E. radiatus* (J. de C. Sowerby) (= *Spirifer lineatus* J. de C. Sowerby), the type species from the 'Wenlock Limestone' of Dudley, English Midlands, was described and reconstructed by St Joseph (1935, p. 322, pl. 15, fig. 10; text-figs 3–4). His description stated that 'The crural bases ... continue as descending lamellae which are slightly divergent and parallel to the inner surface of the dorsal valve. There are about 7–8 whorls and the axis of the spire is directed laterally and slightly posteriorly. A jugum is in the form of a simple arch, located between two descending lamellae and about one-third of the distance from crural bases to anterior margin.' A reconstruction of the brachidium was shown in his paper (St Joseph 1935, pl. 15, figs 10, 12). No serial transverse or longitudinal sections of *E. radiatus* were published by him. Later, Boucot (1963) showed a pair of short jugal processes directed towards the interior of ventral valve at the junction of primary lamellae and crura in *E. radiatus* from the Waldron Shale, Waldron, Indiana (Boucot 1963, pl. 97, fig. 13). He also pointed out (1963, p. 687) that there is no evidence of a band connecting the jugal processes medially. This conclusion is contrary to that made by St Joseph in 1935. The contradiction has not been settled because no relevant illustrations of serial sections of eospiriferines have been published.

Two specimens of *E. radiatus* (Sowerby 1834) from the type horizon at the type locality (Text-fig. 11) and two from the Upper Wenlock of Gotland (Pl. 3, figs 1, 5, 10, 12, 14) were serially sectioned (Text-figs 12, 14). Several specimens identified as *E.* cf. *radiatus* (see Appendix), from the Upper Llandovery of Anticosti, were also selected for sectioning (Text-fig. 16). Reconstructions of the brachidia of British, Swedish and Canadian specimens (Text-figs 13, 15, 17) show that many features of this structure are very similar to that of *E. sinensis* (8–9 whorls of the spiralia in *E. sinensis*, and 8–13 in *E.* cf. *radiatus* (8 whorls) and *E. radiatus* (10 in British specimen and 13 in Swedish specimen)). It should be emphasized that a pair of ventrally acuminated processes is prominent in *E. radiatus* and *E.* cf. *radiatus*, and no band connecting the jugal processes medially is found. This observation is inconsistent with that of St Joseph (1935) but supports Boucot's conclusion (1963).
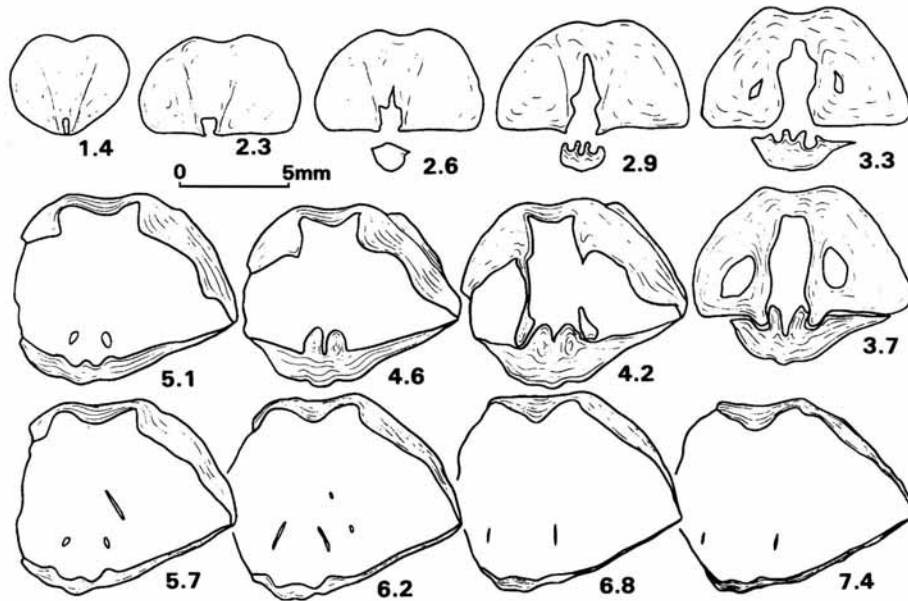
TEXT-FIG. 10. Serial transverse sections of one specimen of *Eospirifer cinghizicus* Borisiak, 1955 (length 13·1 mm, width 17·6 mm?, depth 9·9 mm); NIGP 124770 (18 sections made and 13 selected herein); Lower Llandovery Al'peisskii Horizon, Chinghiz, Kazakhstan.

In addition to *Eospirifer*, three species of *Striispirifer* (with *Hedeina*) were also sectioned to determine internal structures (see Appendix). They are topotype specimens of: (1) *S. acuminiplicatus* Rong, Xu and Yang, 1974 (Text-fig. 18; early Aeronian, Mid Llandovery), herein considered to be one of the earliest known species of *Striispirifer*; (2) *S. plicatellus* (Linnaeus, 1758; Text-fig. 20) (Wenlock) and (3) *S. yunnanensis* Rong and Yang, 1974 (Text-fig. 22; late Ludlow). Reconstructions of their brachidia are shown in Text-figures 19, 21 and 23.

The cross angles of two jugal processes at certain transverse levels (Table 1) are of significance for the general understanding of the brachidium in *Eospirifer* and for evaluating its evolution. They are at about 110–120° in the late Ordovician *E. praecursor*, 70° in earlier Llandovery *E. sinensis*, about 42° in late Llandovery *E.* cf. *radiatus* and 30° in Wenlock *E. radiatus* (Text-fig. 24). It should be emphasized that this reduction of the cross angles of jugal processes through the late Ordovician to Wenlock is recognized only in some species of *Eospirifer*, and not in *Striispirifer* since the cross angles are 30° in the Mid Llandovery *Striispirifer acuminiplicatus*, 80° in the Late Wenlock *S. plicatellus*, and 20° in the Late Ludlow *S. yunnanensis*. Further work on the brachidia in later *Eospirifer* (Ludlow, Přídolí, and Early Devonian) is needed.

The place, on the dorsal side of the crura, near the junction of the crura and primary lamellae, is always smooth and usually somewhat concave dorsally with no sharp geniculation (Text-figs 5, 7, 13, 15, 17, 19, 21, 23). This is probably consistent with Boucot's observation that the crus makes an obtuse angle with the primary lamellae in *Cyrtia*, *Eospirifer*, *Janius*, and *Striispirifer* (Boucot 1963).

With regard to the discussion above, it is verified that a pair of small, centro-ventrally acuminated jugal processes was well-established in the Ashgill and well-developed in most of the Silurian
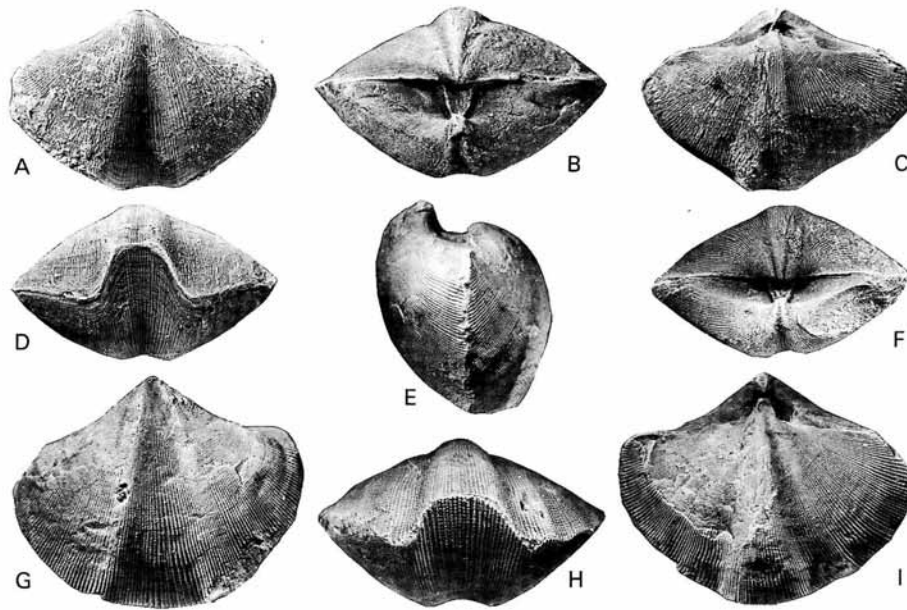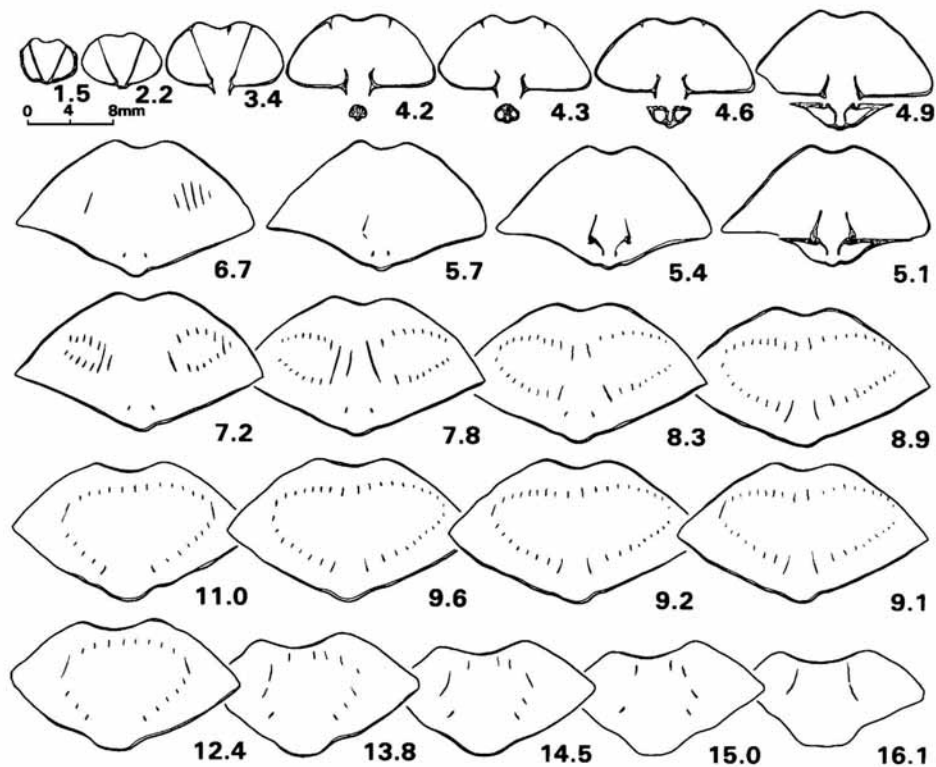
TEXT-FIG. 11. Topotypes of *Eospirifer radiatus* (Sowerby, 1834). A, C, D, F, NIGP 124758a; ventral, dorsal, anterior and posterior views of a conjoined shell; × 1·5, B, E, G–I, NIGP 124759a, posterior, lateral, ventral, anterior and dorsal views of a conjoined shell which has been sectioned for this paper (see Text-figs 12–13); × 2. Much Wenlock Limestone Formation (uppermost Wenlock), Dudley, West Midlands, England.

eospiriferines. No jugum has been found in any specimen of eospiriferine examined herein. It seems unlikely that there was an uncalcified jugum between the two jugal processes. The processes would connect with each other and become a jugum in much later forms of some species in the *Spirifer* group (such as advanced stocks in the Devonian and later). Therefore the form of the brachidium was probably stable during the evolution of the eospiriferines.

Measurements (Table 2; for definitions see Text-fig. 15) of various distances and proportions show: (1) T_1/T is within the range of 98–100 per cent. in different species, with the exception of 95·7 per cent. in a juvenile specimen of *Eospirifer praecursor* (2·9 mm in shell width). We assume this value was significantly stable in the adult stages of many species of eospiriferines. It means that the level of jugal process is located approximately at the level of maximum shell thickness; (2) T_2/T_1 is variable in different taxa (24–41·2 per cent., with the exception of 15 per cent. in a juvenile specimen of *Eospirifer praecursor*) and the value depends on the degree of development of jugal process; (3) L_2/DL is remarkably stable in different species, since all are close to each other within the range 77–87 per cent. (usually 80–85 per cent.), with the exception of 61 per cent. in a juvenile specimen of *Eospirifer praecursor*. The smaller proportion of L_2/DL in the pre-adult stage indicates that it has a significantly smaller lophophore apparatus; (4) L_1/DL is variable in different species, but always within the range 33–45 per cent.

One of the interesting features of this study is the strong asymmetry commonly shown by the spiralia. This asymmetry is much greater than that shown by the shell exteriors. The preservation of most specimens studied is perfect which makes it unlikely that any post mortem mechanical

TEXT-FIG. 12. Serial transverse sections of a topotype specimen of *Eospirifer radiatus* (Sowerby, 1834) (length 19·3 mm, width 24·2 mm, depth 7·45 mm); NIGP 124759a (37 sections made and 24 selected herein); same locality and horizon as for Text-figure 11.

distortion resulting from deformation of the entombing sediments is involved. The state of the complete shells excludes the possibility that asymmetry was due to mechanical injury during life because there is no damage to the shells. Elliott (1958) recognized 'a congenital defect of brachial development', but it can not be proved in fossils, and we agree with Ager and Riggs (1964) that gross distortion of the spiralia would have a harmful effect on a brachiopod's feeding mechanism. Therefore, the asymmetry of the spiralia in eospiriferines is normal and common, and may be seen in the other stocks of the *Spirifer* Group.

COMPARISONS OF EARLY EOSPIRIFERINES WITH OTHER RELATED GROUPS

The early eospiriferines include some of the species assigned to *Eospirifer* and *Striispirifer* (= *Hedeina* Boucot, 1963) known from the upper Ordovician and Lower Silurian (Llandovery). The species attributed to the Early–Mid Llandovery genera, *Yingwuspirifer* Rong, Xu and Yang, 1974, and *Espella* (= *Laevispirifer* Ushatinskaya, 1977), are not discussed herein since no topotype material of these taxa was available for serial sectioning. Material of the type species of the Ashgill genus *Iliella* Rukavishnikova (assigned to the eospiriferines by Nikitin *et al.* 1980) was serially
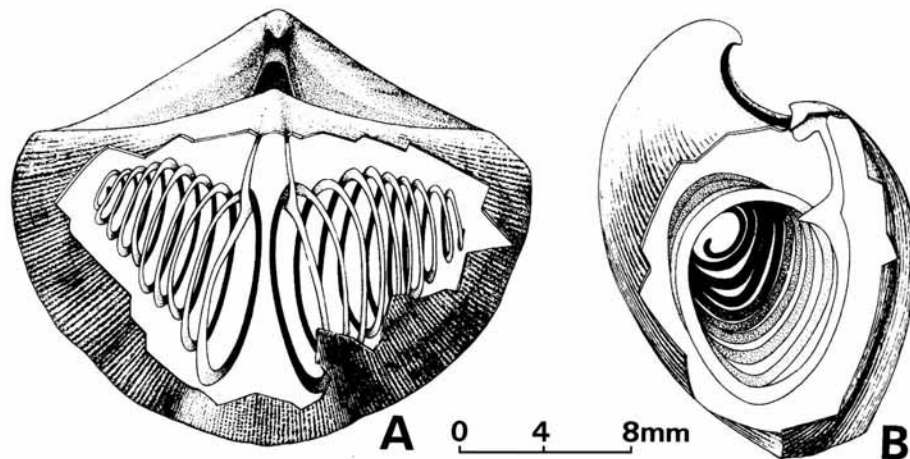
TEXT-FIG. 13. Reconstruction of brachidia of one specimen of *Eospirifer radiatus* (Sowerby, 1834); based on Text-figure 12.

transversely sectioned for this paper but no brachidium was found. However, it seems to the present authors that *Iliella* may be rejected from the eospiriferines because typical early atrypoid cardinalia are present and there is no real ventral interarea on the topotypes of the type species, *Iliella minima* Rukavishnikova, 1980.

Early atrypoids

Although the study of the ontogenetic development of spiralia in eospiriferines is difficult, characters of the brachidium can still be compared with those of the other early spire-bearing groups (atrypoids and athyroids) of the later Ordovician.

A comprehensive study of the spiralia of Caradoc and Ashgill atrypoids was made by Copper (1986). It revealed that the spiralia of Caradoc genera (such as *Manespira* Copper, 1986; *Protozyga* Hall and Clark, 1893; *Idiospira* Cooper, 1956) were primitive and varied. The spiralia of Ashgill genera (such as *Anazyga*, *Zygospira*, *Catazyga*, and *Eospirigerina*) were more complicated, and usually possessed a complete, single-structure, either U-shaped or W-shaped jugum with common features: small and simple spiralia, with their cones directed medially or dorso-medially in fewer whorls. Generally, they have a simple jugum located between the divergent crura in most representatives of the atrypoids. However, *Cyclospira* Hall and Clark, 1893, one of the early atrypoids, ranging from late Caradoc to Ashgill, is an exception (Copper 1986). It is important to compare the brachidium of *Cyclospira* with that of the earliest representatives of eospiriferines since, among all atrypoid genera it is the brachidium of *Cyclospira* that most resembles that of the earliest eospiriferines. We may take two taxa as examples for comparison, *Cyclospira bisulcata* (Emmons, 1842) from the Trenton Limestone (the type horizon is latest Caradoc or earliest Ashgill; Copper 1986) and *Eospirifer praecursor*, the earliest known eospiriferine (mid Ashgill).

The morphology of the crus and brachidium show an essential difference between the two species: the spiralium is directed centrally in *C. bisulcata* (Text-fig. 25, following text-fig. 2 of Copper 1986),

TEXT-FIG. 14. Serial transverse sections of one Swedish specimen of *Eospirifer radiatus* (Sowerby, 1834) (length 24·5 mm, width 32·6 mm, depth 17·5 mm); NIGP 124771 (66 sections made and 24 selected herein); Mulde Beds (SW16) (middle–upper Wenlock), Gotland, Sweden.
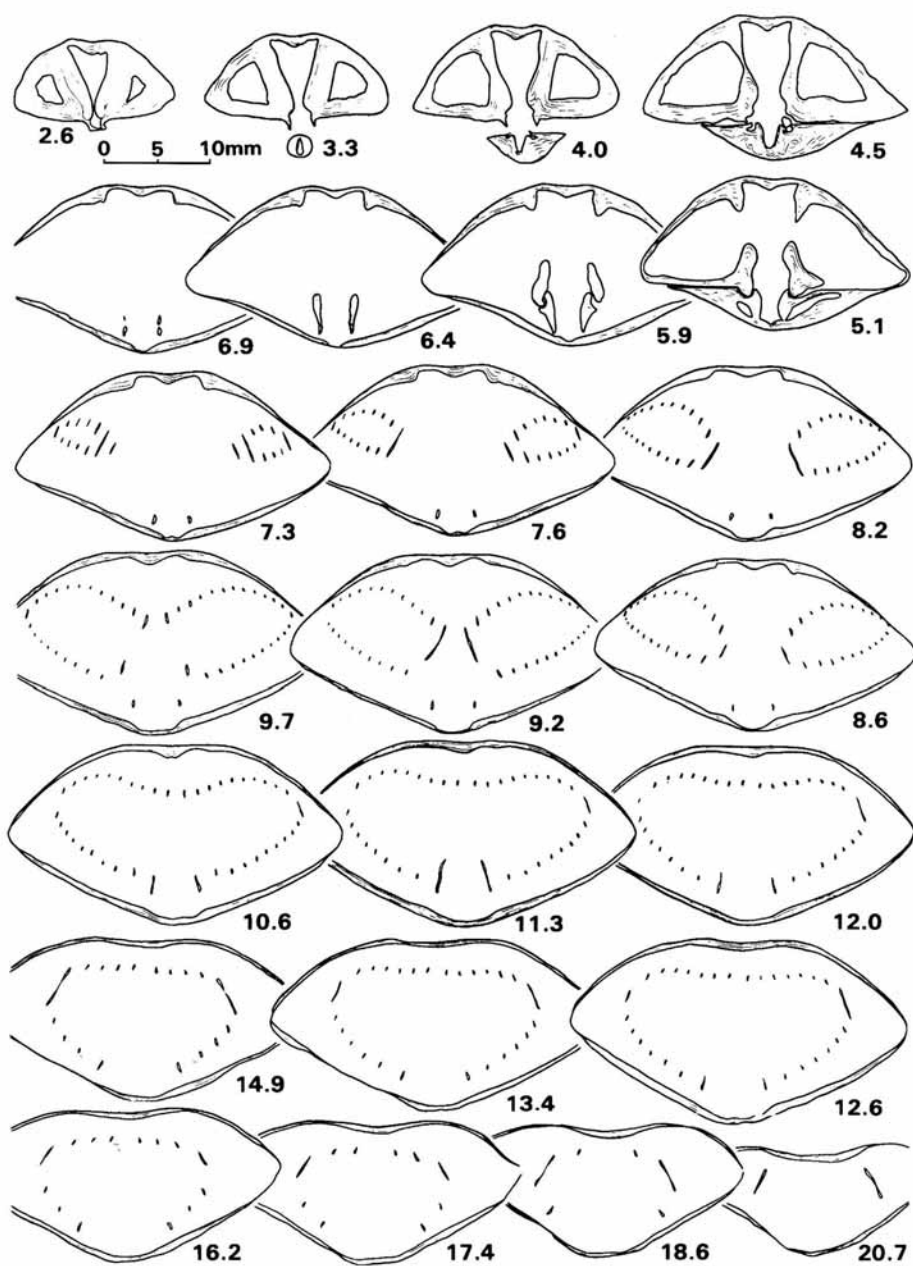
TEXT-FIG. 14. For caption see opposite.
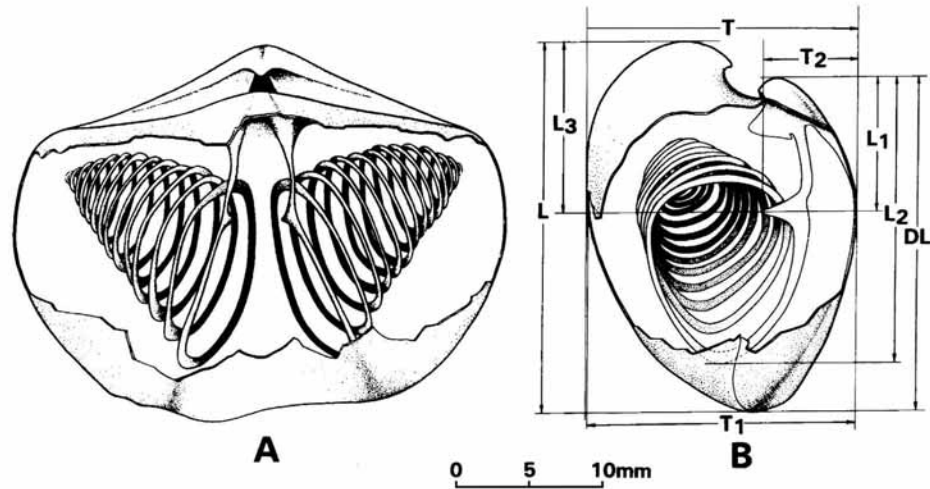
TEXT-FIG. 15. Reconstruction of brachidia of one Swedish specimen of *Eospirifer radiatus* (Sowerby, 1834); based on Text-figure 14.

but laterally in *E. praecursor*. The spiralium is located between two crura in *C. bisulcata*, but outside them in *E. praecursor*; a pair of very small jugal processes is present in *E. praecursor*, but absent in *C. bisulcata*. The differences are so fundamental that these taxa have been assigned to different orders.

There are, however, some remarkable differences between the brachidium of *Cyclospira* and that of other early atrypoid taxa (Copper 1986). One of the most important characters is that the junction between crura and primary lamellae is sharply geniculate in many of the Ordovician smooth or ribbed atrypoids, but is not sharply geniculated in *Cyclospira*. Many early atrypoids have different types of juga, whereas *Cyclospira* has no jugum (Copper 1986, p. 831). Furthermore, it is surprising that some features of the brachidium in *C. bisulcata* are also similar to that of *E. praecursor*, for example: (1) the very small size of the spiralium; (2) the few whorls (one to four) of the spiralium; (3) the slightly divergent crura (with an angle of about 50°) and anteriorly continuous with primary lamellae; (4) the crura is arched ventrally to varying degrees; (5) the junction between crura and primary lamellae is not sharply geniculated; (6) the crura and primary lamellae are located near and parallel to the inner surface of the dorsal valve; (7) the absence of a jugum.

Although some of the similarities mentioned above are probably due to strong similarities in shell size, form and outline (compare Copper 1986, pl. 74, figs 7–21 with Pl. 1, figs 1–12), it seems to us that they are significant in any discussion and evaluation of the origin of the eospiriferines (see below).

Early athyroids

Some of the early athyroids are well-known in pre-Silurian rocks in many places in the world. They are *Hindella* Davidson, 1882, *Cryptothyrella* Cooper, 1942 and *Whitfieldella* Hall and Clark, 1893, known to make their first appearance in the middle Ashgill. Their brachidia are more complex than those of early atrypoids and the brachidia of *Hindella* and *Cryptothyrella* are composed of laterally directed spiralia and a relatively complicated jugum. They are evidently different from *Eospirifer praecursor* in all respects, including the orientation and location of the brachidia.
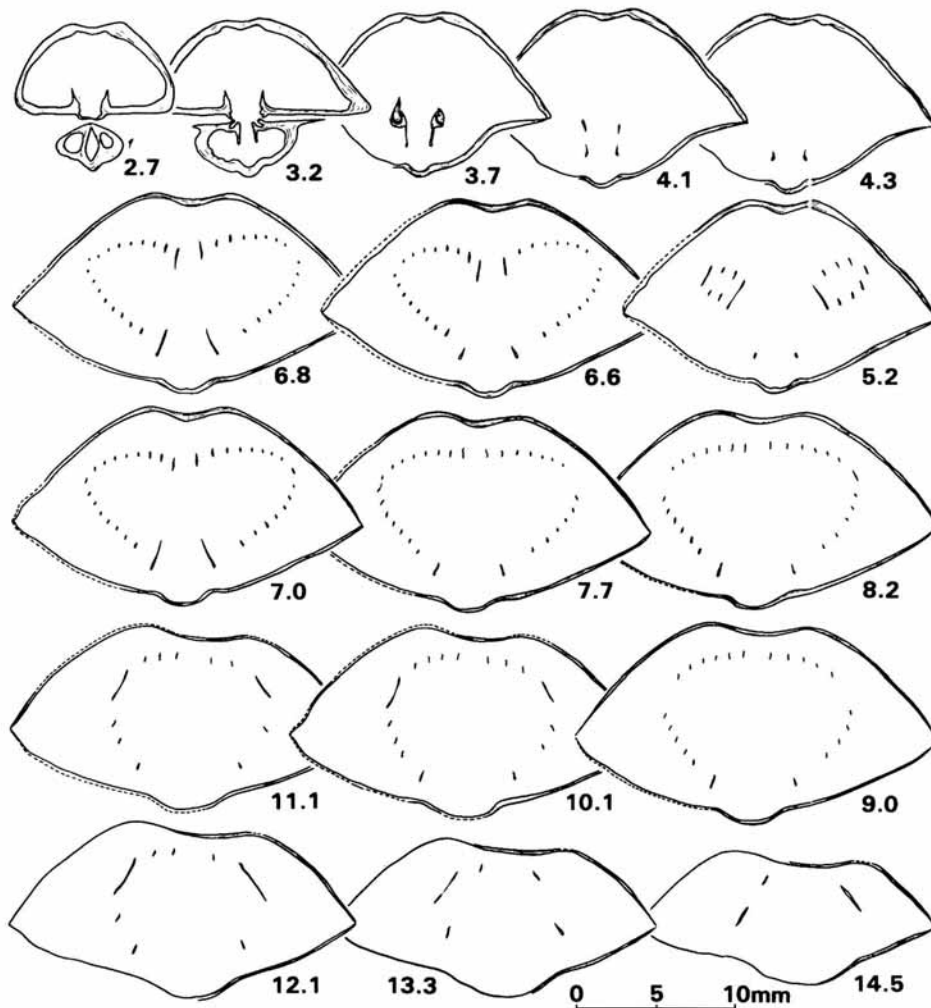
TEXT-FIG. 16. Serial transverse sections of one specimen of *Eospirifer* cf. *radiatus* (Sowerby, 1834) (length 17·7 mm, width 21·2 mm, depth 12·6 mm); NIGP 124772 (33 sections made and 17 selected herein); Jupiter Formation (Upper Llandovery), Anticosti.

A primitive but poorly known athyroid is *Apheathyris* Fu, 1982, from the topmost part of the Pingliang Formation (upper Caradoc), Shijiezigou, Guyuan, Ningxia, North China. It is characterized externally by having a large shell (30 mm long and 29 mm wide), a ventri-biconvex lateral profile and a smooth shell surface. Fu (1982, p. 172, text-fig. 84) made serial sections of a single specimen (the holotype) of *A. guyuanensis* Fu, 1982, the type species of the genus. The sections show that there are small, short, separate socket plates, laterally oriented spiralia with about 11
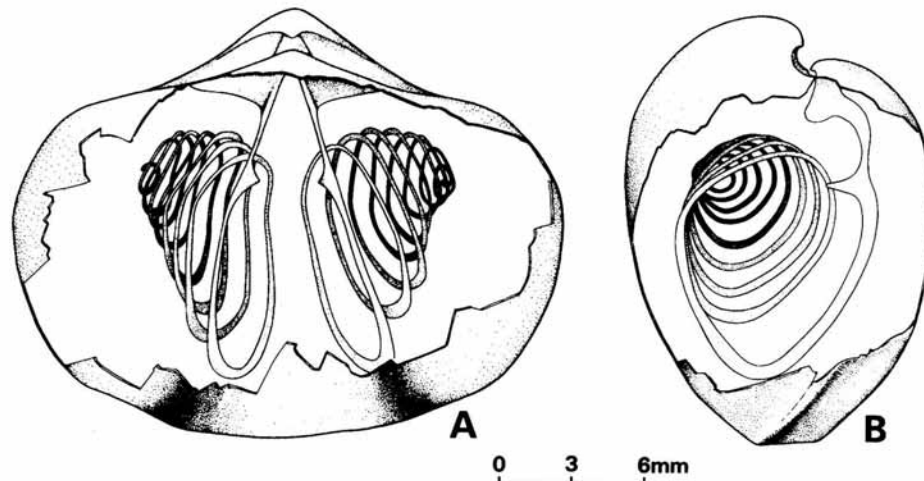
TEXT-FIG. 17. Reconstruction of one specimen of *Eospirifer* cf. *radiatus*; based on Text-figure 13.

whorls, a complicated jugum(?), but no dental plates. Unfortunately, the nature of the jugum and its relationship with the spiralia are unknown. Nevertheless, the internal structures of *Apheathyris* and *Eospirifer* are so fundamentally different that it is reasonable to suppose that the earliest eospiriferines were not derived from the athyroids.

The earliest and poorly known athyroid(?) is *Weibeia* Fu, 1983, from Jinghe Formation (lower Caradoc), Dongzhuang, Liquan, Shaanxi Province, North China. It was assigned to the Meristellidae by Fu (1982, p. 171). This genus possesses a pair of parallel dental plates in the ventral valve and 'brachial plates' in the dorsal valve. However, the assignment of *Weibeia* to the meristellids or other groups is still uncertain since the brachidium of *W. spiriferoides* Fu, 1982, type species of this genus, is unknown and a reliable comparison of the brachidia between *Weibeia* and *Eospirifer* cannot be made at present.

EXPLANATION OF PLATE 3

Figs 1, 5, 10, 12, 14. *Eospirifer radiatus* (Sowerby, 1834); NIGP 124759; same locality and horizon as Pl. 2, figs 13, 18; posterior, anterior, dorsal, lateral and ventral views of conjoined valves; × 1·5.

Figs 3–4, 9, 13, 15, 17, 19–20. *Eospirifer* cf. *radiatus* (Sowerby); same locality and horizon as Pl. 2, figs 10–11. 3–4, 9, 13, 17, NIGP 124761; lateral, dorsal, ventral, posterior and anterior views of conjoined valves, × 1·5. 19, enlargement of posterior part of same specimen in dorsal view showing a complete deltidium; × 8. 15, 20, NIGP 124758; lateral view of conjoined valves and enlargement of posterior part of dorsal view showing a complete deltidium; × 1·5, × 8.

Figs 2, 6, 8, 11, 18. *Eospirifer songkanensis* Wu, 1978; NIGP 124762; topotype; upper part of Shihniulan Formation (upper Aeronian, Middle Llandovery); Hanjiadian, Songkan, Tongzi, north Guizhou, Southwest China; lateral, posterior, dorsal, ventral and anterior views of conjoined valves; × 1·5.

Figs 7, 16. *Eospirifer praecursor* Rong, Zhan and Han, 1994; same locality and horizon as Pl. 1, figs 1–12. 7, NIGP 124755; posterior view of conjoined valves; × 8. 16, NIGP 124757; lateral view of conjoined valves; × 8.

PLATE 3
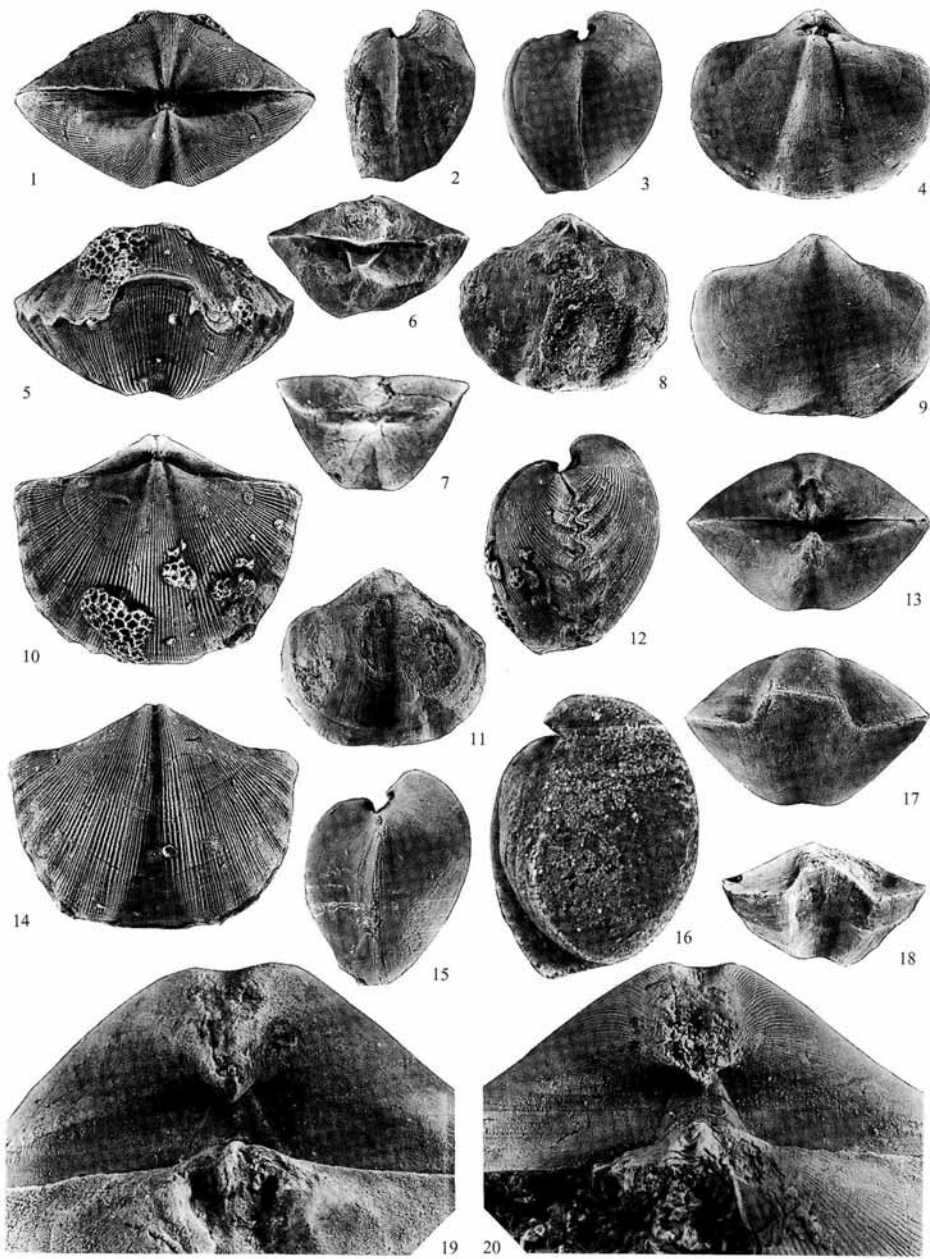
RONG and ZHAN, *Eospirifer*
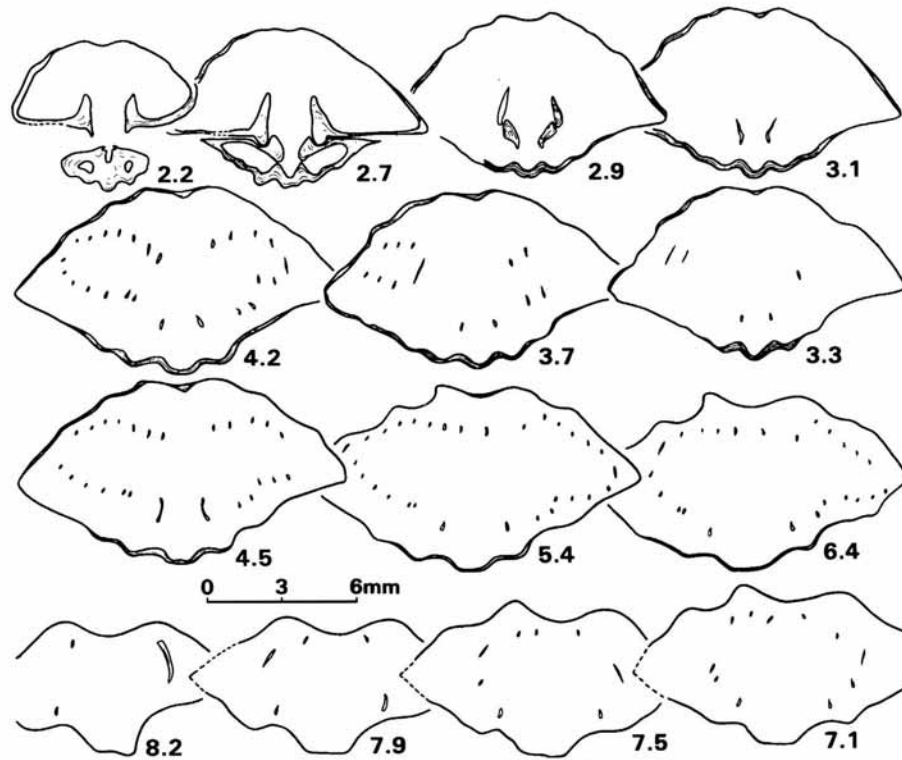
TEXT-FIG. 18. Serial transverse sections of one specimen of *Striispirifer acuminiplicatus* Rong, Xu and Yang, 1974 (length 9·8 mm, width 13·35 mm, depth 7·45 mm); NIGP 124773 (31 sections made and 14 selected herein); Middle Xiangshuyuan Formation (lower Aeronian, Middle Llandovery), Leijiatun, Shiqian, north-eastern Guizhou, South-west China.

DISCUSSION AND CONCLUSIONS

Origin of the eospiriferines

Morphological changes in the cardinalia during the ontogeny of *E. praecursor* led Rong *et al.* (1994) to consider the possibility that the oldest known eospiriferines were derived from an atrypoid stock; a potential ancestor of the eospiriferines could not be identified because of inadequate material (only external and internal moulds were studied). The new material (a large number of conjoined valves) of *E. praecursor* sectioned for this paper now makes it possible to ascertain the nature of its brachidium for further evaluation of the origin of this group.

The microsculpture of *E. praecursor* is of striations so fine that the shell surface often appears to be smooth. The shell size and shape of *E. praecursor* (Pl. 1, figs 1–17) are evidently similar to those of *Cyclospira bisulcata* (compare Copper 1986, pl. 74, figs 7–21). There are also strong similarities between their brachidia, suggesting a closer relationship. In particular, the spiralium of the early growth stages of *E. praecursor* is much more similar to that of the adult stages of *C. bisulcata* than to that of any other known atrypoid genus, although it does not mean that the former must have evolved from the latter.
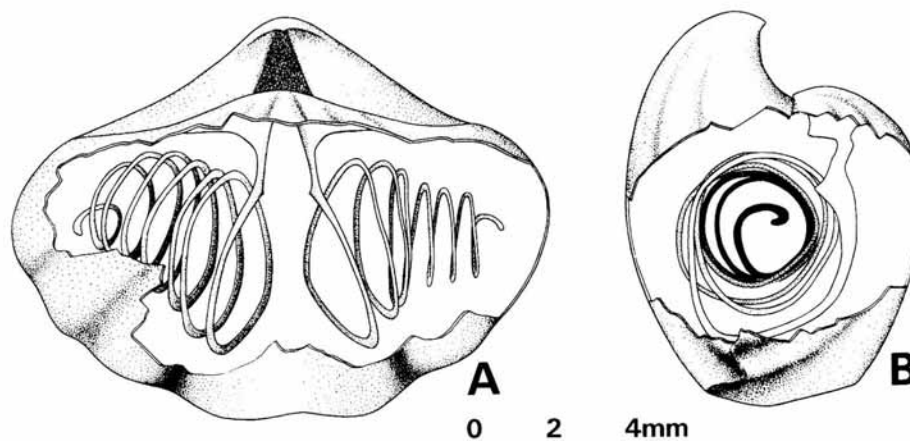
TEXT-FIG. 19. Reconstruction of brachidia of one specimen of *Striispirifer aciminiplicatus* Rong, Xu and Yang, 1974; based on Text-figure 15.

Based on the discussion above, it seems to us that the eospiriferines may have originated from an unknown atrypoid ancestor possessing a centrally directed spiralium. The strophic condition was probably a secondary development accompanying the eversion of the lophophore and the rotation of its arms and their brachidial supports (Williams and Hurst 1977, p. 107). In a population of a *Spirifer* Group species from the Lower Devonian rocks in western Junggar, north-western Xinjiang, Hou Hong-fei, Xu Han-kui and Rong Jia-yu observed in 1990 that larger individuals have, but smaller ones lack, well-developed interareas. Thus the absence and presence of well-defined interareas can occur in different growth stages of the same population of the same species. Therefore, *E. praecursor* may have originated from such atrypoids, as the shells grew to accommodate spiralial spaces changing direction from centrally to laterally. *Eospirifer* and *Cyclospira* might have shared a common ancestor from which *Cyclospira* originated first and *Eospirifer* later, independently.

Discovery of a striated cardinal process in the type species of Eospirifer

The attachment area for the dorsal diductor scars of the eospiriferines was regarded as smooth (Boucot 1963, p. 684), and this feature was considered to be one of the most important bases for the recognition of the eospiriferines (Pitrat 1965, p. H668). The presence of a striated cardinal process has been used for tracing the genera of the group by some authors. *Endospirifer* of Ludlow age (Tachibana, 1981, p. 36) and Cyrtiidae gen.? et sp. nov. of early Ludlow age (Strusz 1984, pp. 125, 140), very similar to *Eospirifer* and *Striispirifer* (with *Hedeina*) respectively, have been defined based on this character; a new cyrtiid genus, *Hedeinopsis* Gourvennec, 1990, more or less like *Striispirifer*, has been established in terms of a striated cardinal process, a delthyrial plate and a deltidial cover. Before 1980, however, some species of the eospiriferines e.g. *Eospirifer*, *Striispirifer*, *Janius*, *Nikiforovaena* and *Cyrtia*, in which a striated cardinal process occur, had been described by Gratsianova (1967, p. 119), Kul'kov (*in* Alekseeva *et al.* 1970, p. 143, text-fig. 83; p. 146, text-fig. 85; p. 149, text-fig. 87), Ivanova (1971, p. 45, pl. 6, figs 4–5, 7), and Rong and Yang (1978, pp. 363–365, text-figs 4–6; pl. 2, figs 23–24, pl. 3, fig. 30). Based on the Chinese material, moreover, Rong and Yang (1978, pp. 364–365) pointed out that (1) the Rhuddanian–Aeronian (Early–Mid Llandovery) eospiriferines e.g. *Eospirifer*, *Yingwuspirifer* and *Striispirifer*, bear a smooth area for diductor attachment at the posterior end of the dorsal valve; (2) *Striispirifer* sp. in the early
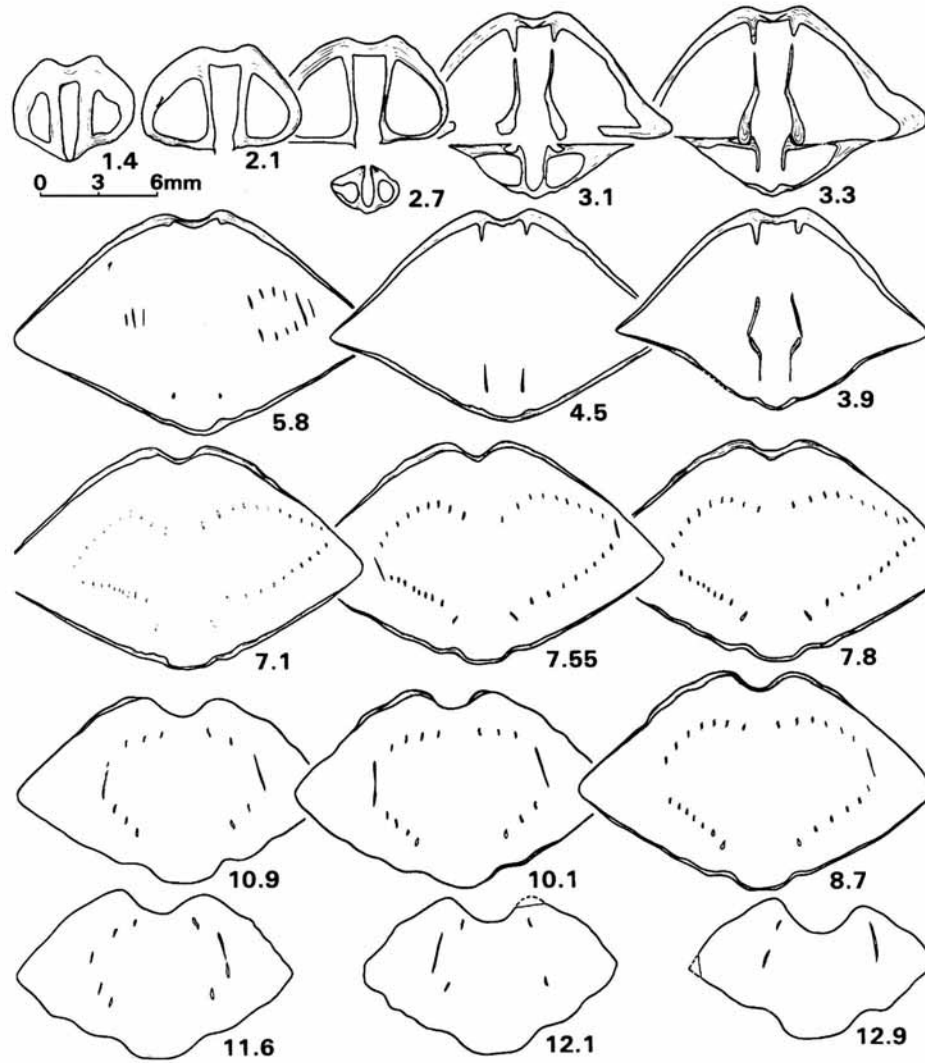
TEXT-FIG. 20. Serial transverse sections of one specimen of *Striispirifer plicatellus* (Linnaeus, 1758) (length 15·0 mm, width 19·7 mm, depth 11·9 mm); NIGP 124765 (39 sections made and 17 selected herein); Much Wenlock Limestone Formation (Upper Wenlock), England.

Telychian (Late Llandovery) possesses rare and fine ridges in the attachment area, indicating an embryonic form of the striated cardinal process; and (3) many species of *Eospirifer*, *Striispirifer* and *Xinanospirifer* in the late Telychian (Late Llandovery) have a well-established striated cardinal
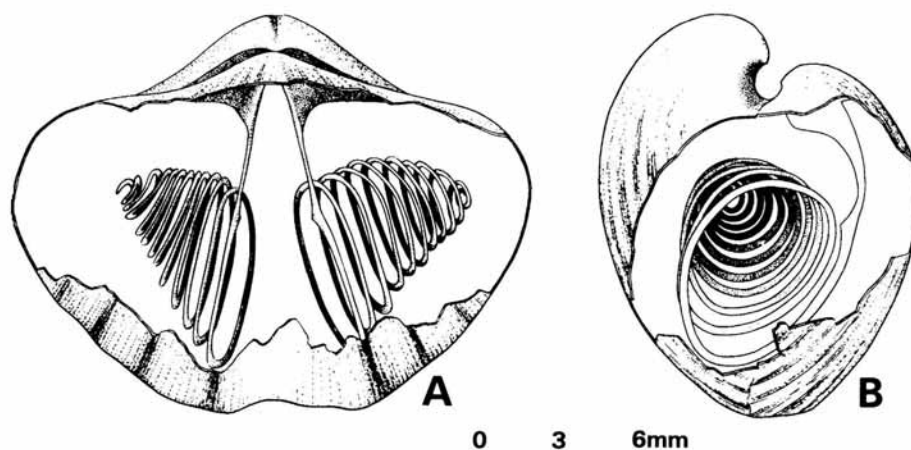
TEXT-FIG. 21. Reconstruction of one specimen of *Striispirifer plicatellus* (Linnaeus, 1758); based on Text-figure 17.

process. This suggests an evolutionary trend within the early eospiriferines. Re-examination of the topotype specimen of the type species of *Eospirifer*, *E. radiatus* (Sowerby) of Wenlock age, re-examined and serially sectioned in this paper, demonstrates that it does possess a comb-like cardinal process (Text-fig. 26). All facts mentioned above indicate that the area for diductor attachment of dorsal valve in the eospiriferines may or may not be comb-like. Thus, the presence or absence of such a cardinal process cannot be regarded as one of the most important and distinctive features in the generic classification of the group.

Evolution of the eospiriferines

The most significant innovations in anatomical design of the *Spirifer* Group at the outset of its history include: (1) a well-developed interarea; (2) a wider and straight hinge-line; (3) a well-defined dorsal fold; (4) fine radial microsculpture; (5) spiralia directed ventro-laterally; and (6) a pair of small jugal processes. The present data and those of Rong *et al.* (1994) indicate that these large-scale evolutionary changes, i.e. early experimentations, were generated during the mid Ashgill (late Ordovician), when the earliest eospiriferines (such as *E. praecursor*) made their first appearance. Subsequently, all of these evolutionary novelties were firmly stabilized probably in all later eospiriferines. They remained stable for more than 50 million years and this can be recognized as a period of evolutionary stasis within the eospiriferines. Thus, these animals seem to have undergone early experimentation in the Late Ordovician and then stabilization later during the Silurian to Mid Devonian.

The general morphology of the skeletal apparatus supporting the lophophores in eospiriferines differs more or less in size and shape, but is basically immutable as regards rotation. The junction between the crura and primary lamellae is smooth and concave ventrally, and a pair of very small jugal processes is present in *E. praecursor*. This is the case with the later taxa studied here, which lack a jugum between the two crura. Once this character was established in the Ashgill species of eospiriferines, there were no remarkable changes in this character until some time during the Devonian, with the exception of the shape of crura: arched ventrally in *E. praecursor* (see Text-fig. 4A, 1.5; 4B, 2.45), but flat in later taxa of eospiriferines (see Text-fig. 6, 8.6). The jugal process in the earliest eospiriferines represents an evolutionary novelty that appeared before the late Ordovician mass extinction event.
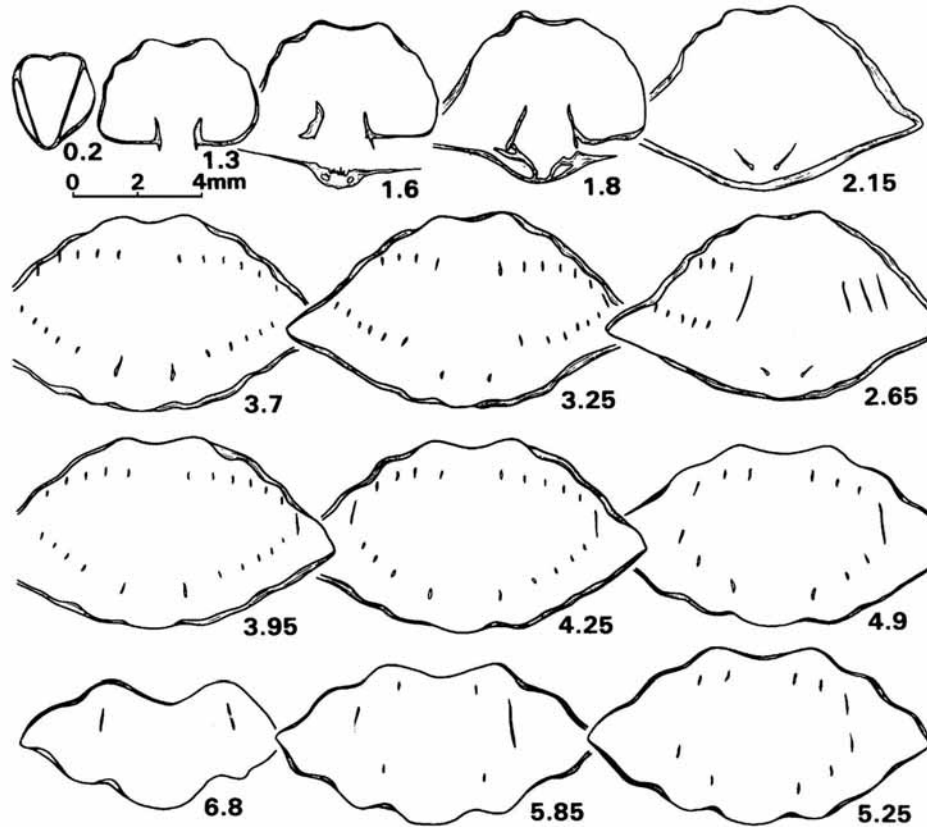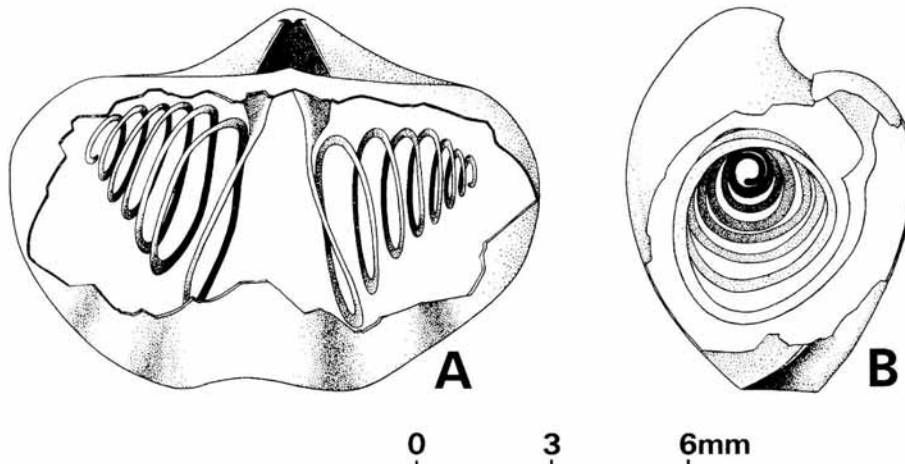
TEXT-FIG. 22. Serial sections of one specimen of *Striispirifer yunnanensis* Rong and Yang, 1978 (length 8·3 mm, width 11·8 mm, depth 6·5 mm); NIGP 124774 (21 sections made and 14 selected herein); Kuanti Formation (Upper Ludlow), Qujing, eastern Yunnan, South-west China.

Almost all large-scale evolutionary innovations occurred immediately after the appearance of the *Spirifer* Group except for the development of crural plates, which probably occurred at the beginning of the Llandovery (the *acuminatus* Biozone). Late Ordovician *E. praecursor* appear to possess no crural plates (Rong *et al.* 1994), whereas *E. tasmaniensis* (Sheehan and Baillie, 1981), from the earliest Silurian, and all other later species of eospiriferines have crural plates. *E.*? sp. (Sheehan and Baillie 1981), from the Arndell Sandstone at Locality F2, Westfield Quarr, Tasmania, is from strata corresponding to the latest Ordovician *persculptus* Biozone (Rong *et al.* 1994) but it is unknown whether it has the crural plates since no dorsal interior of this undetermined species is recorded.

Dispersal of early eospiriferines and their biogeographical significance

Eospirifer is known to be both a Lazarus and successive progenitor taxon which made its first appearance in Asia (East China and ?Kazakhstan) in the mid Ashgill; it disappeared in the

TEXT-FIG. 23. Reconstruction of one specimen of *Striispirifer yunnanensis* Rong and Yang, 1978; based on Text-figure 19.

TABLE 1. Measurements of the cross angle of a pair of jugal processes (α) at a given transverse section level in the following species based on the serial transverse sections examined in this paper. (S: smaller individual; L: larger individual). Note that no jugal processes have been found in *Eospirifer minutus* and *E. songkanensis*.

|	(α)
1. *Eospirifer cinghizicus*	50°
2. *E. praecursor* (S)	70°
3. *E. praecursor* (L)	120°
4. *E. radiatus* (Sweden)	30°
5. *E. radiatus* (England)	35°
6. *E.* cf. *radiatus*	45°
7. *E. sinensis*	70°
8. *Striispirifer acuminiplicatus*	30°
9. *S. plicatellus*	80°
10. *S. yunnanensis*	20°

early Hirnantian (*Normalograptus extraordinarius* Biozone) but appeared in Tasmania in the late Hirnantian (*Glyptograptus*? *persculptus* Biozone) and in Asia (Kazakhstan and South China) and Australia (Tasmania) in the early–mid Rhuddanian (*Parakidograptus acuminatus* to *Cystograptus vesiculosus* biozones). *Eospirifer* did not become extinct at the end of the Ordovician; it had many advanced evolutionary novelties and evolved successively. It appears to have become adapted to shallow marine environmental conditions during the recovery interval (late Rhuddanian to early Aeronian) in some regions of Asia, including South China (Rong and Yang 1978, 1981), Tarim (Rong's identification for the materials of the Kalpintake Formation, provided by Zhang Shi-ben), Kazakhstan (Borisiak 1955; Olenicheva, pers. comm. 1992), and Ningxia, North China (Fu 1985). It did not arrive in Siberia, Avalonia, Baltica, southern Europe, North and South America, and other parts of the world until the late Aeronian (*Monograptus sedgwickii* Biozone) to early Telychian (*Spirograptus turriculatus* Biozone) when the eospiriferines diversified worldwide.
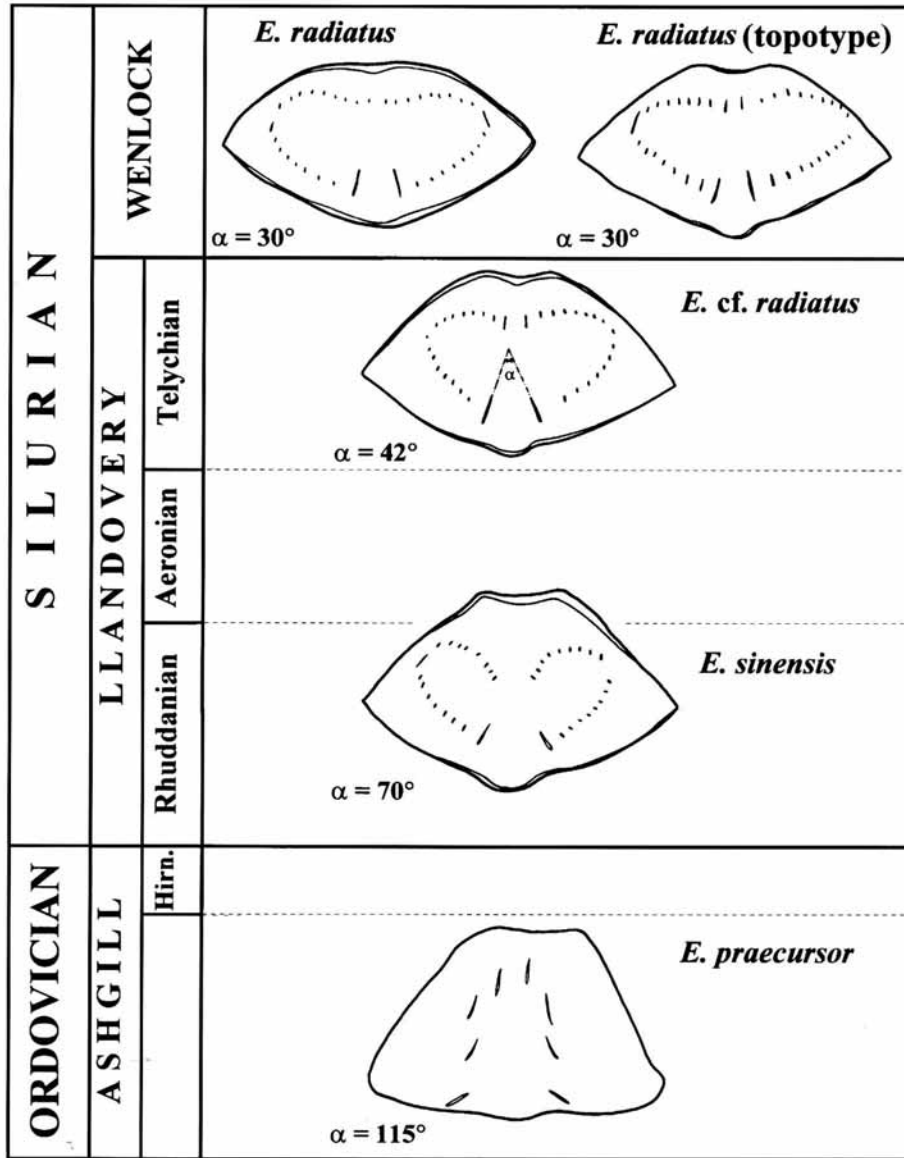
TEXT-FIG. 24. An inferred evolutionary trend in the angle between the jugal process at a given transverse section level in Ashgill, Llandovery and Wenlock species of *Eospirifer*. Hirn. = Hirnantian.

TABLE 2. Measurements of L_1/DL (distance between jugal process/length of dorsal valve), T_1/T (distance of ventral and dorsal valve at the level of jugal process/shell depth), T_2/T_1 (distance between ventral end of jugal process and dorsal valve floor/distance of ventral and dorsal valve at the level of jugal process), L_2/DL (distance between anterior end of spiralium and posterior end of dorsal valve/length of dorsal valve). *Eospirifer praecursor* (s) is a smaller specimen with a 3·1 mm wide shell; *E. praecursor* (l) one of the largest specimens collected with a 6·1 mm wide shell. (For abbreviations, see Text-figure 15).

Taxon	L_1/DL	T_1/T	T_2/T_1	L_2/DL
1. *Eospirifer minutus*	41·6	100	30·7	77
2. *E. praecursor* (s)	33·2	95·7	15·3	86·7
3. *E. praecursor* (l)	45	99·4	41·2	61
4. *E. radiatus* (England)	32·8	98·1	37·2	85·1
5. *E. radiatus* (Sweden)	39·8	99	35·6	84
6. *E.* cf. *radiatus*	32·7	99·5	34·9	82·9
7. *Striispirifer acuminiplicatus*	33	100	36	80
8. *S. plicatellus*	45	98	24	85
9. *S. yunnanensis*	33	100	26	80
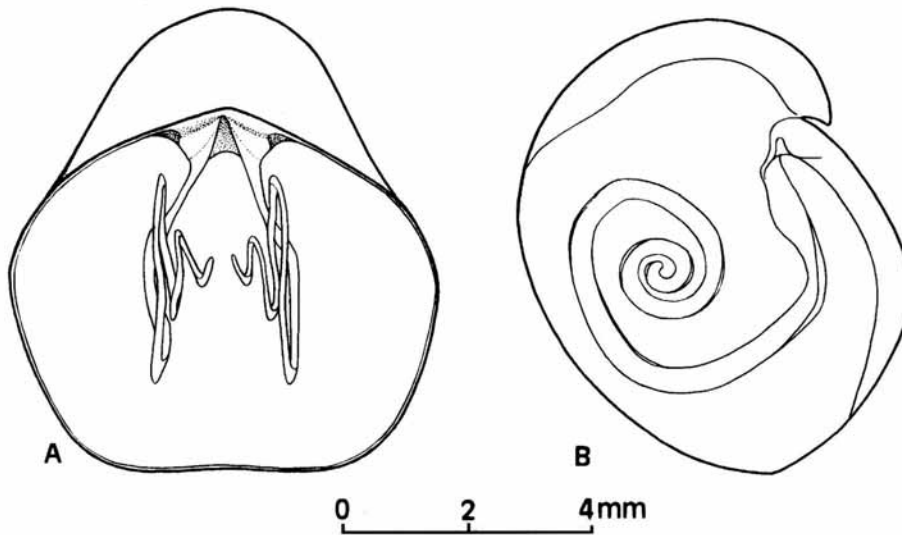
TEXT-FIG. 25. Reconstruction of brachidia of *Cyclospira bisulcata* (Emmons, 1842) from the Hiller Member, Cobourg Formation (upper Caradoc), the type locality, 600 m east-north-east of Rodman, along Gulf Stream, New York (following text-figure 13 of Copper 1986).

This distribution suggests that the tectonic blocks, including South China, Tarim, Alxan, Australia and Kazakhstan, were palaeogeographically located relatively close to each other and could have undergone faunal exchanges by appropriate oceanic current systems. They were probably located more distantly from Siberia, Europe and America during the earlier Llandovery.
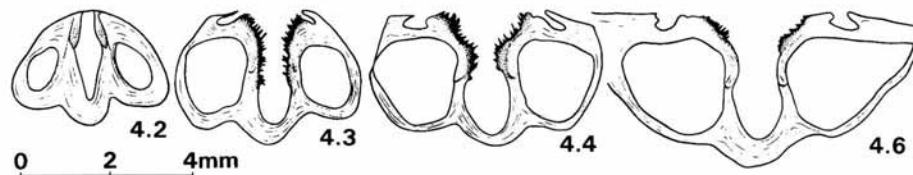
TEXT-FIG. 26. The striated cardinal process in four transverse sections of a topotype specimen of *Eospirifer radiatus* (Sowerby, 1834) (same specimen as used in Text-figure 12).

Suggested environmental model for the origin of the Spirifer *Group*

Jablonski and Bottjer (1990) proposed a pattern of environmental migration for the early history of major post-Palaeozoic clades (at ordinal level), where the first recorded members of the clades were usually confined to inshore sites, with an expansion subsequently across-shelf and in some cases, eventual restriction to deep water slope/basin sites. The *Spirifer* group (Order Spiriferida) is one of the most diverse groups of Brachiopoda in the Phanerozoic and it is worthwhile to test this model using spiriferid data. Accepting the eospiriferines as the most primitive spiriferides, *Eospirifer* as the most primitive eospiriferine, and *E. praecursor* as the earliest known *Eospirifer*, data are available to test Jablonski and Bottjer's model (1990).

All of the type material of *E. praecursor*, from the Changwu Formation (mid Ashgill), Pengli, Jiangshan County, south-western Zhejiang Province, East China, is preserved as internal and external moulds in a yellowish-green mudstone bed (Rong *et al.* 1994). Conjoined valves of this species have been collected from the contemporaneous Xiazhen Formation, Zhuzhai, Yushan County, north-eastern Jiangxi Province, about 32 km south-west of Pengli (see Text-fig. 1). Twenty-nine external and internal moulds of ventral or dorsal valves have been found at Pengli (Rong *et al.* 1994) and a huge number of the individual specimens (nearly 5000) at Zhuzhai. An assignment of *E. praecursor* at Pengli to Lower BA 3 to upper BA 4 was suggested by Rong *et al.* (1994, p. 771), but this is not the case for the occurrence at Zhuzhai. According to a new study of mid Ashgill brachiopod synecology in the Jiangshan–Yushan area, the *E. praecursor* Community has been proposed for an association consisting of the very abundant eponymous species, usually exceeding 99 per cent. of the whole biomass on the same bedding plane (Zhan and Rong 1995). The other

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EXPLANATION OF PLATE 4

Figs 1–2, 6–8, 18, 21, 24–25, 28. *Striispirifer acuminiplicatus* Rong, Xu and Yang, 1974; Lower Xiangshuyuan Formation (lower Aeronian, Middle Llandovery); Leijiatun, Shiqian, north-eastern Guizhou, South-west China. 1–2, 6–8, NIGP 22290, holotype; ventral, lateral, anterior, posterior and dorsal views of conjoined valves; × 3. 18, 21, 24–25, 28, NIGP 44067, topotype; ventral, anterior, posterior, lateral and dorsal views of conjoined valves; × 2.

Figs 3–5, 9, 13. *Striispirifer yunnanensis* Rong and Yang, 1978; NIGP 124763, topotype; Kuanti Formation (Upper Ludlow); Qujing, eastern Yunnan, South-west China; lateral, dorsal, ventral, posterior and anterior views of conjoined valves; × 3.

Figs 10–12, 15–17, 19–20, 22–23. *Striispirifer plicatellus* (Linnaeus, 1758); Wenlock Limestone Formation (Homerian, Late Wenlock); Wenlock Edge, Shropshire, England. 10, 12, 15, 19, 22, NIGP 124764; ventral, lateral, dorsal, posterior and anterior views of conjoined valves; × 1·5. 11, 16–17, 20, 23, NIGP 124765; ventral, dorsal, lateral, posterior and anterior views of conjoined valves, × 2.

Figs 26–27. *Eospirifer* cf. *radiatus*; NIGP 124758, the same specimen as Pl. 2, figs 10–11; posterior and anterior views of conjoined valves; × 1·5.

PLATE 4
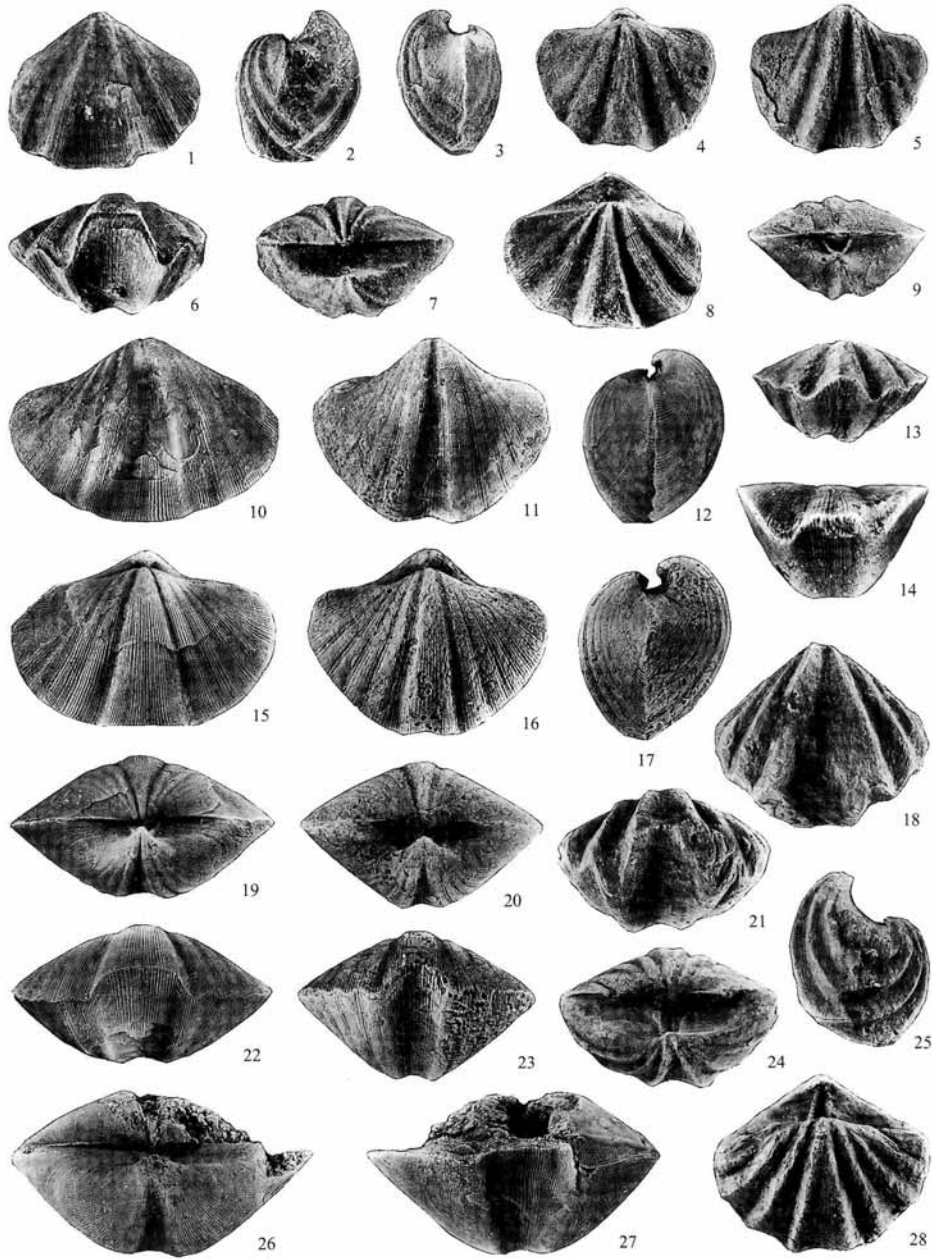
RONG and ZHAN, *Striispirifer, Eospirifer*

members of the community are extremely rare; they include brachiopods (*Ovalospira* and *Antizygospira*), gastropods, bivalves, nautiloids, bryozoans and trilobites. They occur chiefly in calcareous mudstone and micritic limestone. Burrows can be seen in the mudstone. Sometimes, mud-cracks are well developed and a huge number of individuals of *E. praecursor* are present on the bedding plane of the micritic limestone. Rong and Zhan (1995) have suggested an assignment of this community to BA 2, indicating a near shore, very shallow water, normal marine environment with low energy. Although *E. praecursor* was adapted to relatively wide range of environments (through mostly very shallow water (BA 2 at Zhuzhai, most abundant), moderately deeper water (BA 3–4 at Pengli, uncommon), to occasionally deepest water in a low diversity *Foliomena* Fauna (BA 5 at Changwu, very rare)), disparity of numbers of *E. praecursor* in different associations indicates that this taxon may have preferred to inhabit a much shallower water habitat (BA 2) as at Zhuzhai than the relatively deeper water (BA 3–4) at Pengli. If this interpretation holds, it suggests that the Spiriferida originated in nearshore environments.

Conclusions

1. The late Ordovician *Eospirifer praecursor* Rong, Zhan and Han, 1994, is the earliest known eospiriferine and may be considered to be the ancestor of Silurian and Devonian eospiriferines.

2. New evidence confirms the possibility that the eospiriferines originated from a late Ordovician atrypoid stock possessing a simple spiralium directed centrally.

3. *Eospirifer*, a progenitor and Lazarus genus, originated in Asia (East China and ?Kazakhstan) during the mid Ashgill and then migrated into unknown areas (refugia) in the Hirnantian and survived the latest Ordovician mass extinction. It recovered and expanded its range into a number of regions (South China, Qaidam, Tarim, Kazakhstan, and Australia) in the Rhuddanian and early Aeronian, and migrated to Europe and America in the late Aeronian (about *sedgwickii* Biozone) to Telychian.

4. The late Rhuddanian *Striispirifer orbiplicatus* Fu, 1982 (p. 176, pl. 45, fig. 5) from southern Ningxia, north-eastern marginal belt of the Qaidam Plate, and the early Aeronian *Striispirifer acuminiplicatus* Rong, Xu and Yang, 1974 (p. 202, pl. 93, figs 17–19) from north-eastern Guizhou, South-west China, are the two earliest known species of *Striispirifer* (junior synonym *Hedeina*). They are internally very similar to *Eospirifer sinensis* Rong, Xu and Yang, 1974, from the upper Rhuddanian of north-eastern Guizhou, and may have originated from *E. sinensis* by development of rare plications on the flanks.

5. Presence of a striated cardinal process in *Eospirifer radiatus* (Sowerby, 1834), type species of the genus, from the type locality and horizon suggests that it cannot be considered to be an important and distinctive feature for tracing the genera in the eospiriferines.

6. Almost all large-scale evolutionary novelties in the eospiriferines were established at the outset of their history during the late Ordovician when *Eospirifer* originated, indicating that *Eospirifer* is a successive progenitor genus. The eospiriferines seem to have undergone later stabilization in the Silurian and Devonian. Development of crural plates, probably in the earliest Silurian, is a later macroevolutionary change or lag which is of significance in the evolution of the eospiriferines.

7. A probable shallower water environmental model is suggested for the origin of the order Spiriferida.
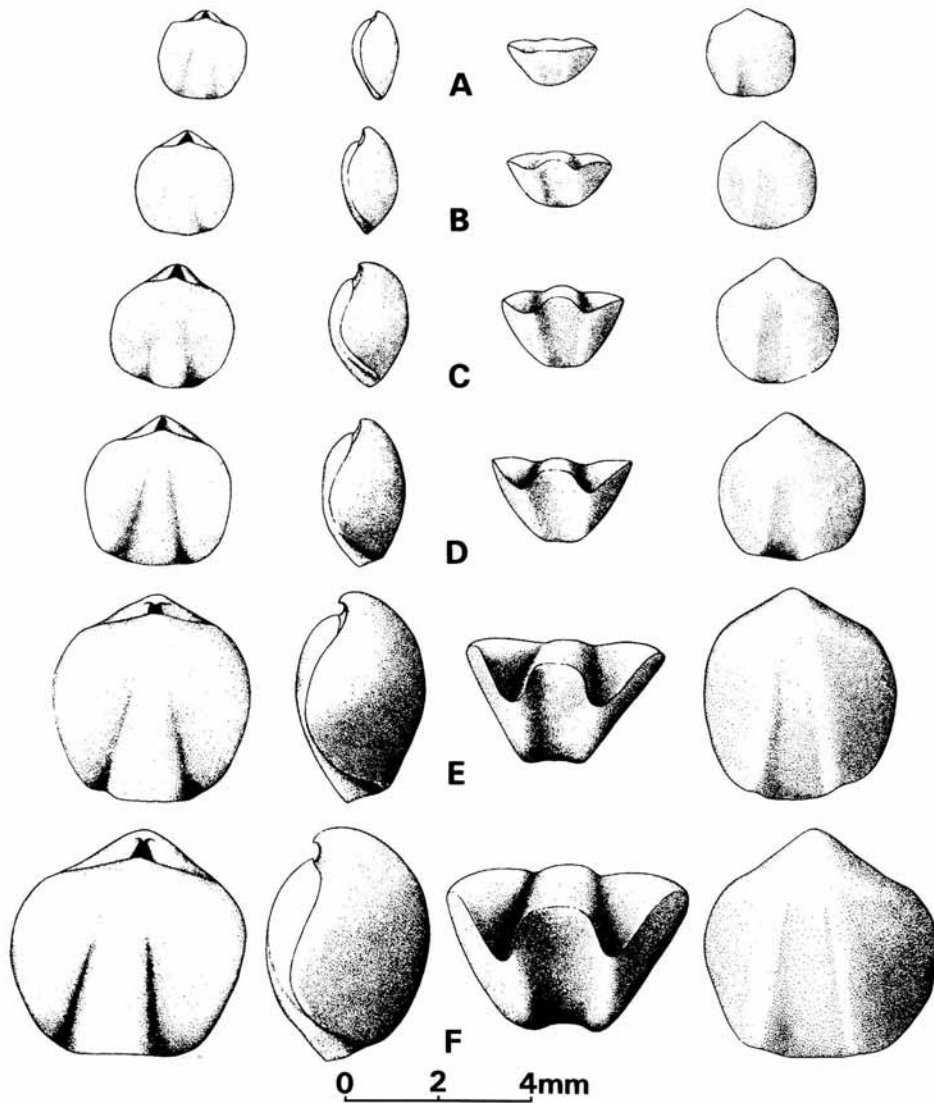
TEXT-FIG. 27. Variations of shell outline, convexity, ventral beak and sulcus in six specimens (A–F) of *Eospirifer praecursor* Rong, Zhan, and Han, 1994, from the Xiazhen Formation (middle Ashgill), Zhuzhai, Qunli, Yushan north-eastern Jiangxi, East China.

SYSTEMATIC PALAEONTOLOGY

Order SPIRIFERIDA Waagen, 1883
Superfamily CYRTIOIDEA Fredericks, 1924
Family EOSPIRIFERIDAE Schuchert and LeVene, 1929
(= HEDEINOPSIDAE Gourvennec, 1991)

Genus EOSPIRIFER Schuchert, 1913

Type species. Eospirifer praecursor Rong, Zhan and Han, 1994.

Eospirifer praecursor Rong, Zhan and Han, 1994

Plate 1, figures 1–17; Plate 3, figures 7, 16; Text-figures 4–5, 27

1994　　*Eospirifer praecursor* Rong, Zhan, and Han, p. 772, figs 9.1–18.

Type locality and horizon. Changwu Formation (middle Ashgill), Pengli, Hejiashan, Jiangshan County, south-western Zhejiang Province, East China.

Materials. Nearly 5000 conjoined valves.

Diagnosis. See Rong *et al.* 1994, p. 772. Lacking crural plates.

Description. The following is based on the conjoined valves.

Exterior. Very small shells, usually 4–5 mm long and wide, 3–3·3 mm deep, the largest known individual 6·5 mm long and wide, 4·5 mm thick; round pentagonal in outline; generally ventri-biconvex in lateral profile, rarely plano-convex or even gently concavo–convex. Ventral beak small, strongly curved; umbo swollen; interarea short, well-developed, slightly to strongly curved; delthyrium small with narrow delthyrial ridges almost perpendicular to the interarea; hinge line straight, about three-quarters or a little more of shell width; dorsal interarea extremely low. Ventral valve strongly convex, about three-quarters to four-fifths of the shell depth; ventral sulcus strongly developed, starting from the apex, shallow, wide, and flat at the base of sulcus, the widest part of the sulcus about half the shell width. Dorsal valve gently convex, sometimes flat or even occasionally slightly concave on the anterior part of the shells; fold prominent but flat, starting anterior to the umbo, lower than flanks, bounded by relatively deep and round furrows. Microsculpture of very fine costellae, generally 14–16 per mm in larger shells (usually 4·5–6 mm in shell width), occasionally 24–25 per mm in very small shells (less than 3 mm in shell width), increasing mainly by bifurcation; concentric lines very rare, if present, most irregular, in particular, near the anterior commissure.

Ventral interior. Teeth small, dental plates fine and short, about one-sixth of the valve length, slightly divergent ventrally.

Dorsal interior. Sockets small, cardinal process non-striate; no crural supporting plates; crura thick and stick-like posteriorly, then plate-like centrally and anteriorly, extending slightly divergently, located close to the dorsal valve, and being smoothly continuous with primary lamellae (= the first half whorl of each spiralium distal from its attachment to crus); a simple spiralium with only three to four whorls, occupying about 50 per cent. of the internal space of both valves in the adult growth stage and extending near the anterior margin; spiralia directed ventro-laterally with the primary lamellae separated, directed slightly divergent and near the sagittal plane; no jugum between two spirally coiled supports for lophophore (Text-figs 4–5).

Variation. Ontogenetic variation within a single population of *Eospirifer praecursor* from the Xiazhen Formation at Zhuzhai, Qunli, Yushan is marked. In addition to those features mentioned above, there are three other aspects as follows: (1) shell outline, generally rounded pentagonal in both smaller and larger specimens but having a slightly elongate circular outline in a small proportion of the individuals; (2) convexity of dorsal valve usually low, about one-quarter of ventral valve convexity, some larger specimens with slightly concave anterior part of dorsal valve, some dorsal valves entirely convex; (3) ventral beak and interarea, from almost erect to curved during its ontogeny: where shell size smaller than 3·5 mm, the beak is almost erect and the interarea

flat, apsacline; where the shell is larger than 3·5 mm, the beak is slightly curved and the interarea also curved, slightly anacline (Text-fig. 27).

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APPENDIX

In this paper serial sections and reconstructions of brachidia are shown for the following species assigned to *Eospirifer* and *Striispirifer* (including *Hedeina*), with the exception of *Eospirifer cinghizicus* and *E. songkanensis*.

Eospirifer
1. *E. cinghizicus* Borisiak, 1955: *cinghizicus* Bed of Al'peisskii Horizon (Llandovery), Chinghiz, Kazakhstan (provided by Dr M. A. Olenicheva; see also Borisiak 1955, p. 68, pl. 12, figs 6–9; and this paper).
2. *E. minutus* Rong and Yang, 1981: the lower–middle Xiangshuyuan Formation (lower Aeronian, Middle Llandovery); Yingwuxi, Sinan County, north-eastern Guizhou Province, South-west China (see also Rong and Yang 1981, p. 372, pl. 1, figs 17–20).
3. *E. praecursor* Rong, Zhan, and Han, 1994: Xiazhen Formation (middle Ashgill), Zhuzhai, Yushan County, north-eastern Jiangxi Province, East China (this paper). The type horizon and locality of this species are upper part of Changwu Formation (middle Ashgill); Pengli, south-west part of Jiangshan County, western Zhejiang Province, East China (see also Rong *et al.* 1994, p. 772, figs 7, 8.2, 9.1–9.18, 10).
4. *E. radiatus* (Sowerby, 1834): topotype, Much Wenlock Limestone Formation (uppermost part of Wenlock, *ludensis* Biozone), Dudley, West Midlands, England (provided by Dr L. R. M. Cocks) (see also St Joseph 1935, p. 322, text-fig. 3 and this paper).
5. *E. radiatus* (Sowerby, 1834): Mulde Beds (SW16) (middle–upper Wenlock), Gotland, Sweden (provided by Dr P. Copper); (see also Boucot 1963, p. 685, pl. 97, figs 1–6; Cocks 1978, p. 161; and this paper).
6. *E.* cf. *radiatus*: Jupiter Formation (C650) (Telychian, Upper Llandovery); Firetower Road, north of Firetower, Anticosti, Canada (provided by Dr P. Copper; this paper). This species is characterized by a complete deltidium covering the whole delthyrium and without any kind of plications at the shell marginal area which can be distinguished from *E. radiatus* (Sowerby) of England.
7. *E. sinensis* Rong, Xu and Yang, 1974: the base of Xiangshuyuan Formation (upper Rhuddanian, Lower Llandovery); Leijiatun, Shiqian County, north-eastern Guizhou Province, South-west China (see also Rong *et al.* 1974, p. 201, pl. 93, figs 34–36; Rong and Yang 1978, p. 371, pl. 1, figs 1–3, 11, 16, 21–26, 29, 33, 34; and this paper).
8. *E. songkanensis* Wu *in* Rong and Yang, 1978: upper part of the Shihniulan Formation (upper Aeronian, Middle Llandovery); Hanjiadian, Songkan, Tongzi, northern Guizhou Province, South-west China (provided by Dr Wu Hao-ruo; see also Rong and Yang 1978, p. 373, pl. 1, figs 27–28, 31–32; and this paper).

Striispirifer
1. *S. acuminiplicatus* Rong, Xu and Yang, 1974: Lower Xiangshuyuan Formation (lower Aeronian, Middle Llandovery); Leijiatun, Shiqian, north-eastern Guizhou Province, South-west China (see also Rong *et al.* 1974, p. 202, pl. 93, figs 17–19; Rong and Yang 1978, p. 375, pl. 1, figs 4–6, 12–15, 30; and this paper).
2. *S. plicatellus* (Linnaeus, 1785): Much Wenlock Limestone Formation (Homerian, Upper Wenlock); Wenlock Edge, Shropshire, England (provided by Dr L. R. M. Cocks; see also Boucot 1963, p. 696, pl. 100, figs 8, 14–15; Cocks 1978, p. 163; and this paper).
3. *S. yunnanensis* Rong and Yang, 1978: Kuanti Formation (Upper Ludlow); Xiaoxiang Reservoir, south-west of Qujing, eastern Yunnan Province, South-west China (see also Rong and Yang 1978, p. 377, pl. 3, figs 26–27, 30; and this paper).