Brachial supporting structure of Spiriferida (Brachiopoda)

Authors: Yuan, Zhiwei, Guo, Wen, Lyu, Dan, and Sun, Yuanlin

Source: Journal of Paleontology, 95(3) : 553-567

Published By: The Paleontological Society

URL: https://doi.org/10.1017/jpa.2020.106

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Paleontology on 18 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Journal of Paleontology, 95(3), 2021, p. 553–567

0022-3360/21/1937-2337
doi: 10.1017/jpa.2020.106

JOURNAL OF PALEONTOLOGY
A PUBLICATION OF THE Paleontological SOCIETY

Brachial supporting structure of Spiriferida (Brachiopoda)

Zhiwei Yuan,[1] Wen Guo,[2] Dan Lyu,[3,4] and Yuanlin Sun[1]*

[1]Key Laboratory of Orogenic Belts and Crustal Evolution, School of Earth and Space Sciences, Peking University, Beijing, 100871, China <yuanzw@pku.edu.cn>, <ylsun@pku.edu.cn>
[2]Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences and Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing, 210008, China <wenguo@nigpas.ac.cn>
[3]Research Institute of Petroleum Exploration and Development, PetroChina, Beijing, 100083, China <lvdan@petrochina.com.cn>
[4]Key Laboratory of Oil and Gas Reservoir, China National Petroleum Corporation, Beijing, 100083, China

Abstract.—The filter-feeding organ of some extinct brachiopods is supported by a skeletal apparatus called the brachidium. Although relatively well studied in Atrypida and Athyridida, the brachidial morphology is usually neglected in Spiriferida. To investigate the variations of brachidial morphology in Spiriferida, 65 species belonging to eight superfamilies were analyzed. Based on the presence/absence of the jugal processes and normal/modified primary lamellae of the spiralia, four types of brachidium are recognized. Type-I (with jugal processes) and Type-II (without jugal processes), both having normal primary lamellae, could give rise to each other by losing/re-evolving the jugal processes. Type-III, without jugal processes, originated from Type-II through evolution of the modified lateral-convex primary lamellae, and it subsequently gave rise to Type-IV by evolving the modified medial-convex primary lamellae. The evolution of brachidia within individual evolutionary lineages must be clarified because two or more types can be present within a single family. Type-III and Type-IV are closely associated with the prolongation of the crura, representing innovative modifications of the feeding apparatus in response to possible shift in the position of the mouth towards the anterior, allowing for more efficient feeding on particles entering the mantle cavity from the anterior gape. Meanwhile, the modified primary lamellae adjusted/regulated the feeding currents. The absence of spires in some taxa with Type-IV brachidium might suggest that they developed a similar lophophore to that in some extant brachiopods, which can extend out of the shell.

Introduction

Brachiopods are a group of marine benthic filter-feeding organisms using cilia aligned on the tentacles of the lophophore to capture food particles from seawater (James et al., 1992; Strathmann, 2005). Studies of recent brachiopods have classified the shape of the lophophore into several types, such as ptycholophe, plectolophe, and spirolophe (Rudwick, 1962, 1970; Emig, 1992; Williams et al., 1997a). The spirolophe, in which the tips of the brachia diverge from each other to form a pair of freely coiled spirals, occurs in many modern inarticulates, rhynchonellides, and possibly the terebratulide genus *Leptothyrella* Muir-Wood in Muir-Wood et al., 1965 (Muir-Wood, 1965; Emig, 1992). This type of lophophore is also thought to have been present in fossil inarticulates, rhynchonellides, atrypides, athyridides, spiriferides, and spiriferinides (Rudwick, 1970). In particular, the last four groups have calcareous spiralia to support their lophophore, perhaps dealing with a more complex feeding system.

The classification of the spire-bearing brachiopods (atrypides, athyridides, spiriferides, and spiriferinides) has been revised many times since Davidson's (1882) first proposal, which emphasized the direction of spiralia and the presence/absence of jugal structures. Although the taxonomic ranks of spire-bearers have been modified several times, initially classified as families (Davidson, 1882; Waagen, 1883), then suborders (Boucot et al., 1965; Ivanova, 1972), and finally in the orders of modern classifications (Cooper and Grant, 1976b; Carter et al., 1994, 2006; Alvarez and Rong, 2002; Copper, 2002; Carter and Johnson, 2006), the diagnostic characteristics differentiating the groups have never changed. Other features of the brachidia, such as development of the jugal structures and number of coils within spiralia, are also of diagnostic significance within the suprageneric groups in Atrypida and Athyridida. However, the morphology of brachidia has never been considered significant in the intra-classification of Spiriferida. Instead, shell form, ornamentation, cardinalia, and other structures have been considered more important (Boucot et al., 1965; Waterhouse, 1968, 1998; Havlíček, 1971; Carter, 1974; Archbold and Thomas, 1986; Goldman and Mitchell, 1990).

By the time the punctate Spiriferinida was raised to the order level (Cooper and Grant, 1976b), the brachidium had wholly lost its taxonomic significance within the suprageneric groups in Spiriferida (Carter and Johnson, 2006) and was rarely taken into account. Thus, descriptions of the brachidia,

---

*Corresponding author

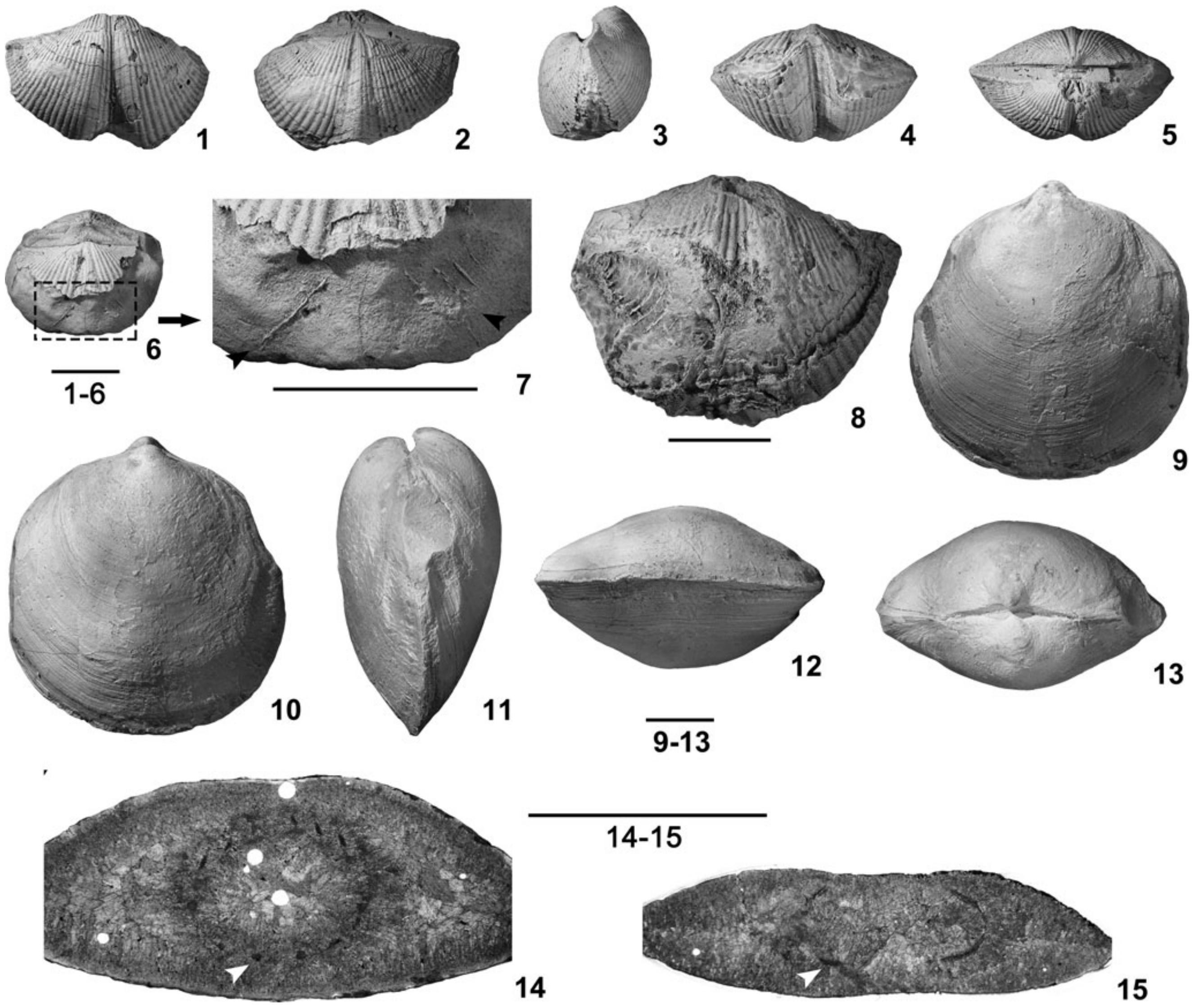

Figure 1. (**1–8**) *Eochoristites neipentaiensis*: (**1–5**) PKUM 02–0930, ventral, dorsal, lateral, anterior, and posterior views; (**6, 7**) PKUM 02–0929, dorsal view (**6**) and (**7**) enlargement of anterior region; arrow on the left side of (**7**) indicates the primary lamellae; arrow on the right side of (**7**) indicates the first whorl of spiralium; (**8**) PKUM 02–0931, ventral view showing posterolaterally directed spiralium on the left side. (**9–15**) *Weiningia ziyunensis*: (**9–13**) PKUM 02–0925, ventral, dorsal, lateral, anterior, and posterior views; (**14, 15**) transverse sections of PKUM 02–0850 (23.75 mm long); distances from the tip of ventral beak are 17.00 mm (**14**) and 20.20 mm (**15**); arrows indicate the change from rod-like crura to plate-like primary lamellae. Scale bars represent 10 mm.

especially for the primary lamellae and spiralia, were usually incomplete in numerous investigations (e.g., Campbell, 1961; Carter, 1972, 1974, 1985; Cooper and Dutro, 1982; Chen et al., 2006; Zhang and Ma, 2019). One reason for neglecting brachidia may be attributed to their limited preservation because this calcareous support for the lophophores is very fragile and easily damaged or even completely destroyed by the post-mortem filling of shell interiors with coarse sediment and subsequent diagenetic processes. The techniques used to visualize the internal structures (e.g., acid etching of silicified specimens, serial sectioning) are also time-consuming and the results are sometimes hard to interpret, therefore many studies have been focused on the umbonal region of the specimens to investigate the morphologies of cardinalia and crura only.

Despite the difficulties in recognizing brachidial features, we describe the morphological variations in the spiralia that support the lophophore and its connection structure to the cardinalia (crura), suggesting several types of brachidium. The distribution of these types of brachidium within the suprageneric groups is examined and the possible phylogenic relationship between these brachidia is discussed.

Materials and methods

The brachidium data in this study included 63 spiriferide brachiopod species recorded in the literature and two spiriferide brachiopod species (*Eochoristites neipentaiensis* Chu, 1933 and *Weiningia ziyunensis* Yuan et al., 2019; Fig. 1; Table 1) studied herein. The data selected from the literature are mainly based on whether a publication includes a restoration of the brachidium, figured serial sections, or figured specimens that clearly show or describe the crura and brachidium of the selected

Table 1. Information on the two spiriferide species sectioned in this study.

Taxa	Specimen number	Sectioning direction	Horizon and age	Location
Eochoristites neipentaiensis Chu, 1933	PKUM 02-0929	Transverse	Yingtang Formation; upper Tournaisian, lower Carboniferous	Jiguanshan, Guilin, Guangxi Province, China (25°34′52.92″N, 106°22′10.68″E)
Weiningia ziyunensis Yuan et al., 2019	PKUM 02-0850	Transverse	Baizuo Formation; Serpukhovian, lower Carboniferous	Near Zongdi, Ziyun County, Guizhou Province, China (25°35′5.64″N, 106°22′7.2″E)
	PKUM 02-0926	Transverse		
	PKUM 02-0927	Transverse		
	PKUM 02-0928	Longitudinal		

taxon. Unfortunately, many taxa that were described with spiralia in the literature are not compiled into the current dataset because most of their brachidial information is limited to the direction of the spiralia and coiling number, and the figured serial sections of specimens, if present, inadequately represent the complete brachidium. The serial sections of *E. neipentaiensis* and *W. ziyunensis* were recorded as both digital images and acetate peels and drawn from the digital images under the software CorelDRAW-X6. The images of the specimens and sections were taken using a Nikon SM1500 stereomicroscope equipped with a Nikon DS-Fi3 microscope camera and Nikon Eclipse Lv100pol microscope equipped with a Nikon DXM1200F camera, respectively. Sixty-five species belonging to 34 genera, 17 families, and eight superfamilies were analyzed (Supplemental Table 1).

In this study, we followed Williams and Brunton's (1997) definitions of crura, primary lamellae, and spiralia. The crura are paired rod- or plate-like processes extending from the cardinalia or septum that support the posterior end of the lophophores, and their distal ends are prolonged into the plate-like primary lamellae of the spires in the extinct spire-bearing stocks. The spiralia are a pair of spiral lamellae in the spire-bearing brachiopods (equal to the brachidia), representing outgrowths from the crura, extending well into the mantle cavity and supporting the lophophores, while the primary lamellae are the first half whorls of each spiralium distal from their attachment to the crura.

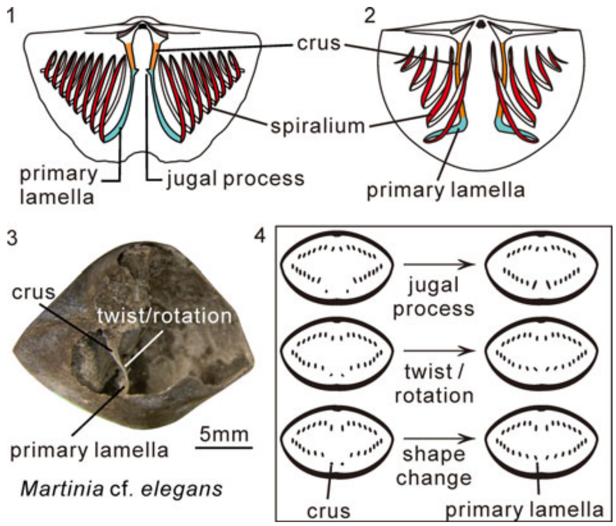

Figure 2. Diagrammatic drawing showing generalized brachidial types and segments, as well as morphological changes at crura-primary lamellae junction. (**1**) Normal brachidium; (**2**) modified brachidium; (**3**) twist/rotation at crura-primary lamellae junction, photographed from the specimen (NIGP143574) used in Shen and Clapham, 2009; (**4**) morphological changes at crura-primary lamellae junction in succeeding serial sections.

To investigate variations of the brachidia in Spiriferida, the morphological features of the crura, primary lamellae, and subsequent spires were examined for each of the selected taxa, including the direction (divergent/convergent/subparallel) and shape (rod-like/plate-like) of the crura and primary lamellae, the crura type (normal/prolonged), and the starting position and direction of the primary lamellae. The direction (posterolateral/lateral), spiral alignment, and coiling number of the spiralia were examined as well. Normal crura refer to those supporting the spiralia posterodorsally, while the prolonged crura refer to those extending to or even beyond the anterior margin of the spiralia (Fig. 2.1, 2.2).

When the crura extend forward in level dorsal to the spiralia to merge with the primary lamellae, there will be jugal processes, twists or rotation, attenuation, ventral bending, and even shape changes in the cross-section. These morphological features and changes were used to determine the boundary of the two different elements in this paper (Fig. 2.3, 2.4).

As several previous studies have revealed, congeneric species, such as those of *Crurithyris* George, 1931 (Cooper and Grant, 1976a; Brunton, 1984; Sun and Baliński, 2011), *Eospirifer* Schuchert, 1913, and *Striispirifer* Cooper and Muir-Wood, 1951 (Rong and Zhan, 1996), basically share the same pattern of crura and brachidia (i.e., the type of crura and primary lamellae, configuration of jugal processes and spiral cones, and probably the direction of the spiralia). Here, *E. minutus* Rong and Yang, 1978, is considered to have jugal processes similar to other species of *Eospirifer* because the weak geniculation at the junction between crura and primary lamellae (Rong and Zhan, 1996, fig. 9) may in fact represent the rudimentary jugal processes. Variation of the brachidia in the spririferides discussed in this paper is mainly concerned with the generic rather than specific level characteristics, although there are exceptions.

Repository and institutional abbreviation.—All illustrated and sectioned specimens in this study are housed in the Geological Museum of Peking University (PKUM), Beijing, China.

Results

Crura and brachidium morphologies of Eochoristites neipentaiensis *and* Weiningia ziyunensis.—As the type species of *Eochoristites* Chu, 1933, *E. neipentaiensis* is a characteristic and widely recognized index brachiopod species for the early Carboniferous (Tournaisian) deposits in South China (Jin, 1961; Yang, 1964; Yang et al., 1977; Tan, 1987; Sun and Baliński, 2011). Weathered and sectioned material (Figs. 1.6–

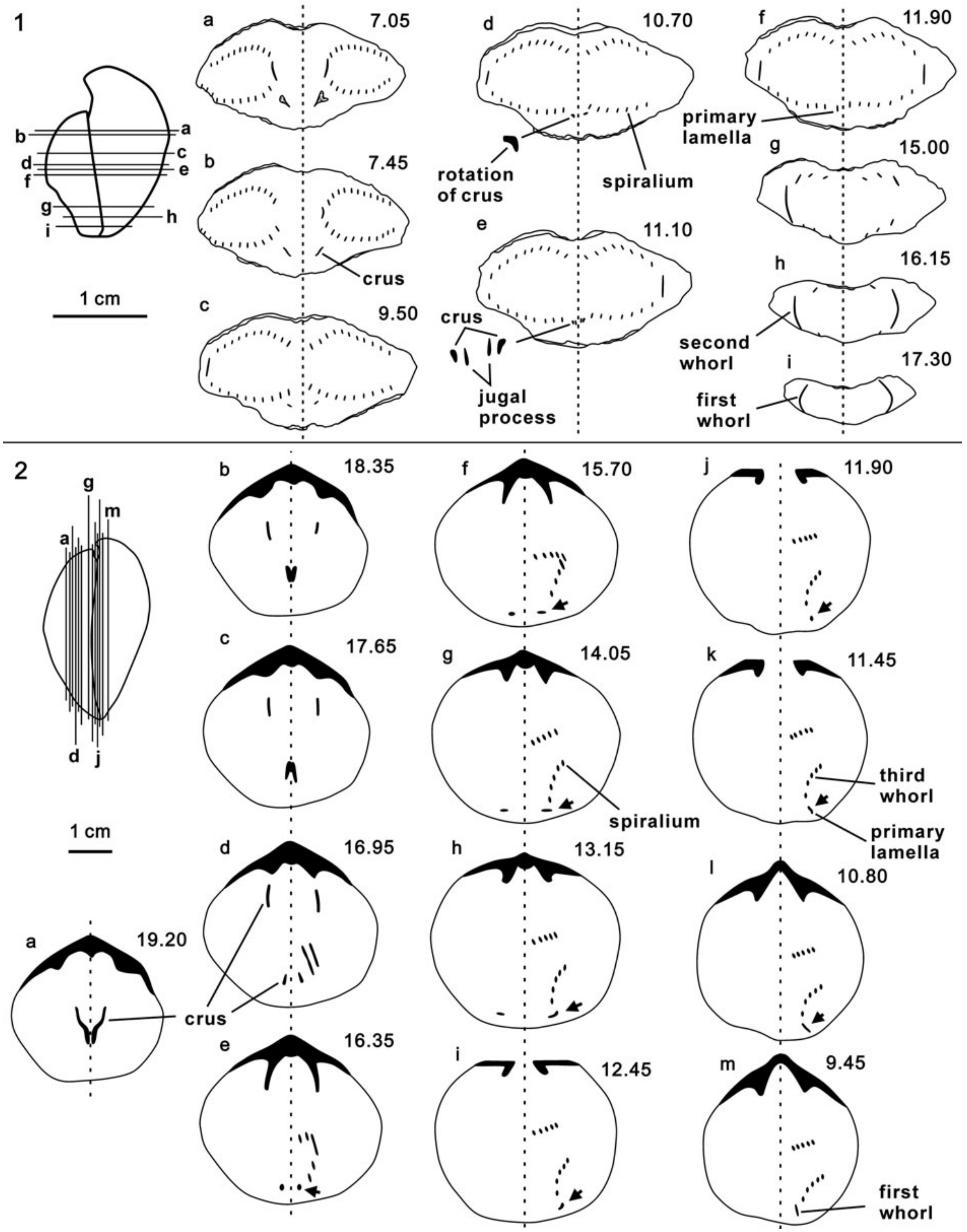

Figure 3. Transverse serial sections of *Eochoristites neipentaiensis* (posterior view) and longitudinal serial sections of *Weiningia ziyunensis* (dorsal view): (**1**) *Eochoristites neipentaiensis*, PKUM 02–0929 (24 sections made and 9 selected herein). Distances measured in millimeters from the tip of ventral beak. Dash lines represent the symmetry planes of shell. (**2**) *Weiningia ziyunensis*, PKUM 02–0928 (27 sections made and 13 selected herein). Distances measured in millimeters from the most convex part of ventral valve. Dashed lines represent the symmetry planes of shell. Arrows indicate the changes from rod-like crura to plate-like primary lamellae (16.35–10.80 mm).

1.8, 3.1) from the Guilin area reveals paired plate-like crura that are ventrolaterally inclined and sub-parallel, becoming slightly convergent to the anterior, and give rise to the primary lamellae near the mid-point of the dorsal valve (Fig. 3.1d–f). Very small and probably posteriorly pointed jugal processes are observed in the junction between the crura and primary lamellae (Fig. 3.1e).

The primary lamellae are plate-like and divergent toward the anterior (Fig. 1.7). The spiralium is posterolaterally directed (Figs. 2.8, 3.1), containing 11–16 whorls. The brachidial restoration of this species is given in Figure 5.

Weiningia ziyunensis is a newly named species of the family Martiniidae from the lower Carboniferous Baizuo Formation (Serpukhovian) of Ziyun County, Guizhou Province (Yuan et al., 2019). The serial sections and restoration of its brachidium show that the crura are rod-like and very long, and exhibit a repetition of divergence and convergence from the crural bases to the front of the spiralia (Figs. 3.2d, 3.2e, 4, 5.3). The primary lamellae can be distinguished from the rod-like crura by their plate-like cross-sections (Figs. 3.2e–g, 4.1j–m, 4.2g–j, 4.3d–f). Starting from the distal end of the crura, the primary lamellae run some distance lateroventrally and then reversely flex towards the mid-line, forming semi-circular loops that are laterally convex and perpendicular to the commissural plane in front of the spiral cones (Figs. 3.2j–m, 4.1m, 4.1n, 4.2j, 4.2k, 4.3h. 5.3, 5.4), after which they turn posteriorly near the mid-line to produce the rest of the spires (Fig. 5.4). This is peculiar among the spiriferide brachidia. Spiralia are located relatively close to the anterior of the shell, with their posterior margins slightly behind the mid-valve. Spiral cones are directed posterolaterally, usually containing 10–14 whorls.

Variations of the crura and brachidium in the selected spiriferide brachiopods.—Among the selected taxa, most possess normal crura that are generally restricted in the posterior part of the shell (e.g., *Eospirifer*, *Eochoristites*; Fig. 5.1, 5.5), but in *Weiningia* Jin and Liao, 1974, *Attenuatella* Stehli, 1954, *Biconvexiella* Waterhouse, 1983, *Curicella* Grant, 1976, *Crurithyris*, and *Orbicoelia* Waterhouse and Piyasin, 1970, the crura are prolonged and can extend to the anterior part, or even in front of the spiralia (Fig. 5.3, 5.10–5.16). The crura can be rod- or plate-like in different taxa, but are exclusively rod-like when prolonged. The crura also can be divergent, convergent, or sub-parallel towards the anterior in different genera, and seem to be consistent among congeneric species. For example, the crura are divergent in *Eospirifer* and *Striispirifer* (Rong and Zhan, 1996) and sub-parallel in *Crurithyris* (Brunton and Champion, 1974; Cooper and Grant, 1976a; Brunton, 1984; Sun and Baliński, 2011; Fig. 5.11, 5.15). In *W. ziyunensis*, the crura display a repetition of divergence and convergence (Fig. 5.3). At the junction between the crura and primary lamellae, there is a twist or rotation in taxa such as *Eochoristites*, *Spinocyrtia* Frederiks, 1916, *Martinia* M'Coy, 1844, *Neospirifer* Frederiks, 1924, and *Gypospirifer* Cooper and Grant, 1976a (Ager and Riggs, 1964; Fig. 2.3), evident jugal processes in *Eospirifer*, *Striispirifer*, and *Anthracothyrina* Legrand-Blain, 1984 (Rong and Zhan, 1996; Shi et al., 2016), and a change from being rod-like to plate-like in *Crurithyris*, *Ladjia* Veevers, 1959, and *Weiningia* (Ma, 2009; Figs. 3.2, 4, 5.9, 5.11).

Compared to the crura, the primary lamellae exhibit more variation in terms of the configuration of jugal processes and curvature types. The jugal processes are medioventrally or posteroventrally directed and have been described in some of the selected taxa, such as *Eospirifer*, *Striispirifer*, *Martinia*, and *Lepidospirifer* Cooper and Grant, 1969 (Cooper and Grant, 1976a; Rong and Zhan, 1996; Fig. 5.5). Among all superfamilies, only the genera belonging to Cyrtospiriferoidea, Ambocoelioidea, and Reticularioidea are not equipped with jugal processes, but this may reflect the limited number of taxa examined in detail. The cross angle between the paired jugal process, which was previously used to describe the angle between these structures in the cross-section (Rong and Zhan, 1996), is variable among different genera, such as *Eospirifer*, *Striispirifer*, *Anthracothyrina*, *Costispirifer* Cooper, 1942, and *Johndearia* Waterhouse, 1998 (Hall and Clarke, 1894; Campbell, 1961; Rong and Zhan, 1996; Shi et al., 2016). According to those species in *Eospirifer* recorded by Rong and Zhan (1996), this angle could be variable among congeneric species as well.

In most studied taxa, the primary lamellae run anteroventrally from the distal ends of the crura, and keep a consistent course and morphological trend with the subsequent spires (Fig. 5). This kind of primary lamellae is called the normal type herein. In some ambocoeliines and *Weiningia*, the primary lamellae initiate anterior to the spiral cones and display different forms. From the distal ends of the crura, they run lateroventrally in *Crurithyris* and *Weiningia*, and medioventally in *Attenuatella*, *Biconvexiella*, *Curicella*, and *Orbicoelia*, representing two modified types of primary lamellae—lateral- and medial-convex, respectively. After extending into the ventral valve, the primary lamellae in *Crurithyris* gradually go posteriorly into the spires (Fig. 5.11, 5.16), while those in *Weiningia* reversely flex towards the mid-line to form semi-circular loops in front of the spires (Fig. 5.3, 5.4). This may suggest that the primary lamellae in *Weiningia* are more complex than those in *Crurithyris*, although the primary lamellae in both genera are regarded as lateral-convex type. As for *Attenuatella*, *Biconvexiella*, *Curicella*, and *Orbicoelia*, the primary lamellae in *Curicella* run into spires medioventrally (Grant, 1976), whereas those in *Attenuatella*, *Biconvexiella*, and *Orbicoelia* exhibit S-shaped curvatures (Waterhouse, 1964; Fig. 5.10, 5.14), indicating the simple medial-convex primary lamellae in *Curicella* and the complex ones in the other three ambocoeliines. In addition, the well-preserved specimens of *Crurithyris* in Cooper and Grant (1976a), Brunton (1984), and Sun and Baliński (2011) clearly show that the primary lamellae in this genus are evidently wider than the subsequent spiral lamellae (Fig. 5.11, 5.12, 5.15). Similar widening primary lamellae are also observed in *Attenuatella*, *Biconvexiella, Curicella*, and *Orbicoelia* (Waterhouse, 1964; Armstrong, 1968; Cooper and Grant, 1976a, b; Grant, 1976; Jin and Sun, 1981; Fig. 5.10–5.16). Thus, widening of the primary lamellae can be considered an important synapomorphy of these ambocoeliines.

In Spiriferida, the coil number of spiralia is highly variable, ranging from a few to >20. For example, Ager and Riggs (1964) recorded at least 25 whorls of the spiralium in *Spinocyrtia*. This feature is generally dependent on the growth stage, shell size, and shape. Although the coil number of spiralia is expected to vary from one species to another, the spiral coil is nearly absent in *Attenuatella* and *Biconvexiella*. This was shown in some specimens that were carefully examined by Armstrong (*B. convexa* Armstrong, 1968) and Cooper and Grant (1976a, *A. attenuata* Cloud, 1944); thus the absence of spiral coil in the two genera

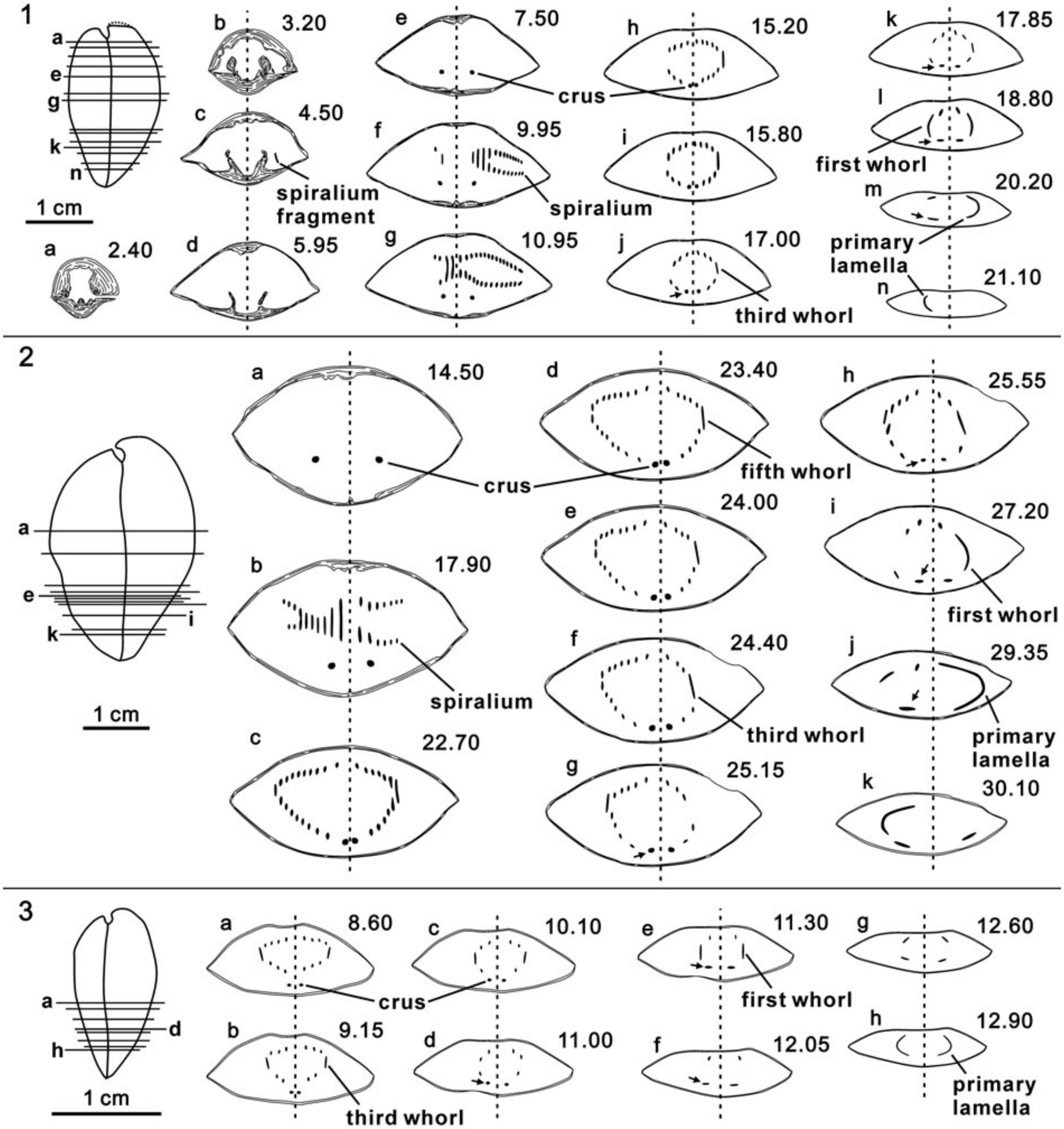

Figure 4. Transverse serial sections of *Weiningia ziyunensis* (posterior view): (**1**) PKUM 02–0850 (31 sections made and 14 selected herein); (**2**) PKUM 02–0926 (44 sections made and 11 selected herein); (**3**) PKUM 02–0927 (28 sections made and 8 selected herein). Distances measured in millimeters from the tip of the broken (**1**) and complete (**2, 3**) ventral beaks. Dashed lines represent the symmetry planes of shell. Arrows indicate the changes from rod-like crura to plate-like primary lamellae: 17.00–20.20 mm in (**1**), 25.25–29.35 mm in (**2**), 11.00–12.05 mm in (**3**).

should be attributed to reduced spiralia, possibly reflecting paedomorphosis rather than aplasia in ontogenetic growth.

The spiralia are directed posterolaterally toward the cardinal extremities in most of the studied taxa, such as those in *Eochoristites* and *Eospirifer* (Fig. 5.1, 5.5), and laterally directed in some smooth spiriferides with subovate-to-round shell outline (e.g., *Weiningia* and *Emanuella* Grabau, 1923) (Fig. 5.3, 5.6). Lee et al. (2019a) recently reported ventrally directed spiralia in the Permian spiriferellide brachiopod *Spiriferella protodraschei* Lee and Shi in Lee et al., 2019b. Their reconstruction revealed that each spiralium in the specimen is almost uniform in diameter and does not show the apically tapering pattern, and they appear to have directly developed from strong and anteriorly extended crura. Based on the extraordinary orientation and form of the spiralia, the authors suggested that this species likely had developed a considerably modified feeding pattern similar to that of the living rhynchonellides. However, the direction of the spiralia in this species probably needs further study because the possibility of a degree of post-mortem distortion could not be completely ruled out due to the constraints posed by the single specimen. For this reason, its crura and brachidium are not considered in our discussion.

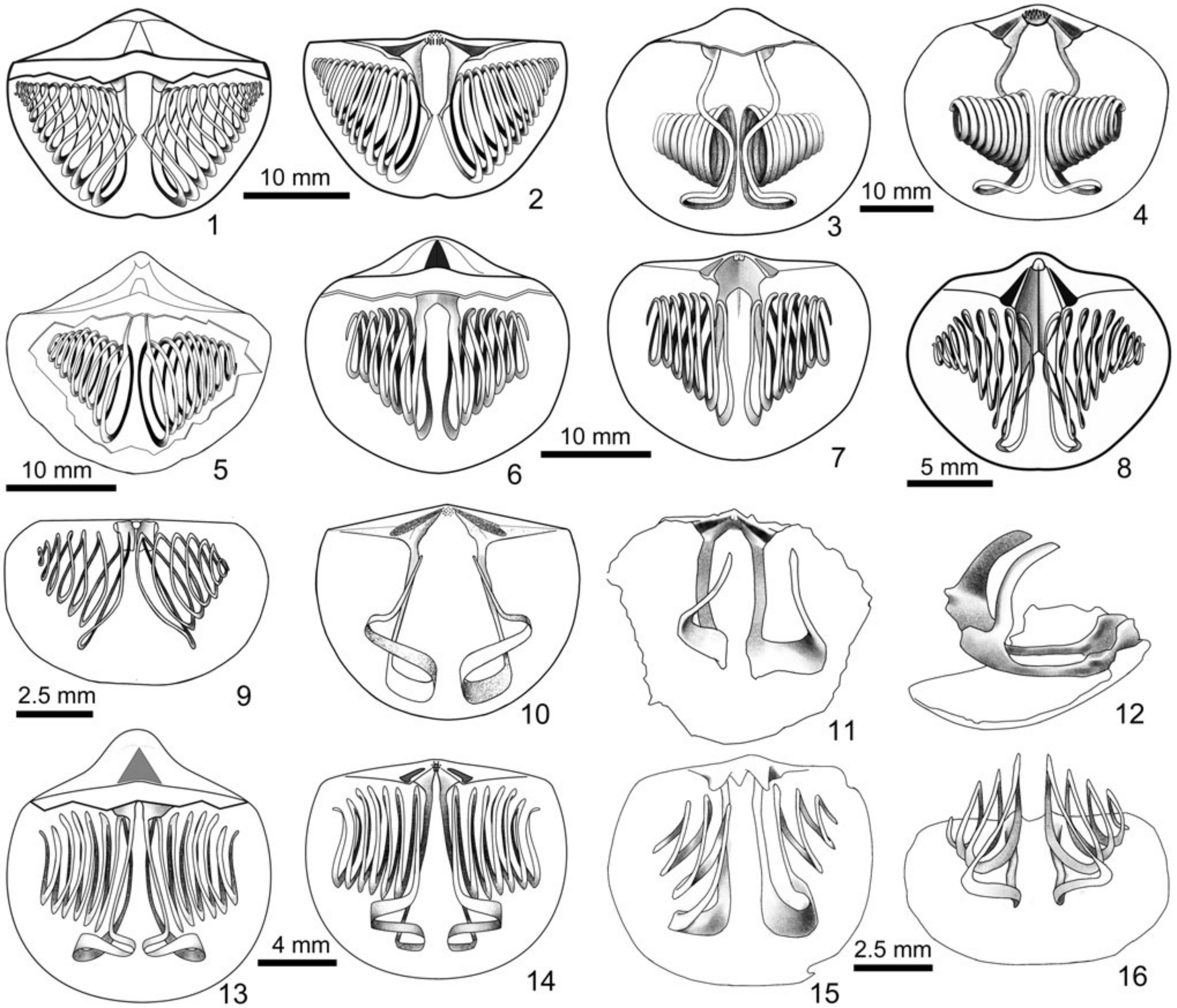

Figure 5. Reconstruction of the brachidia of selected spiriferide taxa. (**1, 2**) *Eochoristites niepentaiensis*, dorsal and ventral views; (**3, 4**) *Weiningia ziyunensis*, dorsal and ventral views; (**5**) *Eospirifer radiatus* (Sowerby, 1834), dorsal view, redrawn from Rong and Zhan (1996, fig. 13); (**6, 7**) *Emanuella plicata* Grabau, 1931, dorsal and ventral views, based on serial sections in Zhang (2016); (**8**) "*Emanuella*" *meristoides*, ventral view, based on serial sections in Caldwell (1968, fig. 4); (**9**) *Ladjia* sp., ventral view, redrawn from Ma (2009); (**10**) *Biconvexiella convexa*, ventral view, redrawn from Armstrong (1968); (**11, 12**) *Crurithyris urei* (Fleming, 1828), ventral and lateral views, drawing from Brunton (1984, fig. 90a, b); (**13, 14**) *Orbicoelia speciosa* (Wang, 1956), dorsal and ventral views, based on serial sections in Jin and Sun (1981); (**15, 16**) *Crurithyris tumibilis* Cooper and Grant,1976a, drawing from Cooper and Grant (1976a, pl. 590, figs. 50, 52).

Discussion

Types of brachidium in Spiriferida.—Given the variations of the primary lamellae and spiralia discussed above, the brachidia in Spiriferida can be assigned to the normal and modified groups according to the configuration of the jugal processes and spires, as well as types of the crura and primary lamellae (Fig. 5). The number of spiral coils, which varies not only within species during ontogeny (Rong and Zhan, 1996) but also among species (Table 2), is not considered significant. Similarly, the direction of the spiralia is also of little importance for its low variability. The normal group dominates in the studied taxa and is represented by shells with the normal primary lamellae that are supported by the normal crura, with or without the jugal processes. The modified group is less common and characterized by the absence of jugal processes and the modified (lateral- and medial-convex) primary lamellae that are supported by the prolonged crura.

The normal group can be divided into Type-I and Type-II based on the presence or absence of the jugal processes. The former possesses jugal processes, normal primary lamellae, and spiral coils (Fig. 5.1). This type is found in *Eospirifer*, *Striispirifer*, *Eochoristites*, *Martinia*, *Anthracothyrina*, *Neospirifer*, *Gypospirifer*, *Lepidospirifer*, *Spiriferella* Chernyshev, 1902, and *Costispirifer* (Table 2). Type-II, with normal primary lamellae and spiral coils, is distinguished from Type-I by the absence of the jugal processes. This type includes a large proportion of taxa not only within the normal group but also in all studied taxa, including *Spinocyrtia*, *Orthospirifer* Pitrat, 1975, *Ambocoelia* Hall, 1860, *Ambothyris* George, 1931, *Emanuella*,

Table 2. Brachidium structure of the selected taxa in Spiriferida Waagen, 1883. TS = transverse shape, JCP = junction between crus and primary lamella, JP = jugal process, TPL = type of primary lamella, CNS = coil number of spiralium, TB = type of brachidium, SR = stratigraphic range.

	Crus							
Taxa	TS	Type	JCP	TPL	CNS	TB	SR	Main reference
Eospirifer	rod	normal	attenuation; JP	normal	3–12	I	O_3^2–D_2^1	Rong and Zhan, 1996
Striispirifer	plate	normal	JP	normal	7–11	I	S_1^1–S_3^1	Rong and Zhan, 1996
Eochoristites	plate	normal	rotation; attenuation; JP	normal	13–14	I	D_3^2–C_1^1	this study
Spinocyrtia	plate	normal	rotation	normal	25	II	D_2	Ager and Riggs, 1964
Orthospirifer	plate	normal	rotation	normal	21	II	D_2^2–D_3^1	Pitrat, 1975, 1977
Ambocoelia	plate/rod	normal	rotation/attenuation	normal	4–7	II	D	Hall and Clarke, 1894; Goldman and Mitchell, 1990; Zhang and Ma, 2019
Attenuatella	rod	prolonged	attenuation	medial-convex	0	IV	P_1^3–P_3	Waterhouse, 1964; Cooper and Grant, 1976a, b
Biconvexiella	rod	prolonged	attenuation	medial-convex	0	IV	P	Armstrong, 1968
Cruricella		prolonged	attenuation	medial-convex	2	IV	C_2–T_1	Grant, 1976
Crurithyris	rod	prolonged	attenuation	lateral-convex	5	III	D_3^1–P	Brunton, 1984; Cooper and Grant, 1976a
Orbicoelia	rod	prolonged	attenuation	medial-convex	8	IV	P	Jin and Sun, 1981
Ambothyris	rod	normal	attenuation	normal	≥6	II	D_2^1-D_3^1	Zhang and Ma, 2019
Emanuella	plate/rod	normal	rotation/attenuation	normal	6–8	II	D_2^1–D_3^1	Goldman and Mitchell, 1990; Li and Jones, 2007; Zhang, 2016
Ladjia	rod	normal	attenuation	normal	7	II	D_2^2–D_3^1	Ma, 2009
Xiangia	rod	normal	attenuation	normal	2–3	II	D_3^1	Lü and Ma, 2017
Elythyna	plate	normal	rotation	normal	11	II	D_1^3–D_2^2	Li and Jones, 2007
Martinia	plate	normal	rotation; JP	normal	**>16**	I	C_1^2–P	M'Coy, 1844; Shen and Clapham, 2009
Weiningia	rod	prolonged	attenuation	lateral-convex	10–14	III	C_1^3–C_2^1	this study
Martiniopsis	plate	normal	rotation	normal	18–19	II	C_2–P	Brown, 1953
Anthracothyrina		normal	JP	normal	12	I	C_1^2–C_1^3	Shi et al., 2016
Neospirifer	plate	normal	rotation; JP	normal	19	I	C_2–P	Cooper and Grant, 1976a
Crassispirifer	plate	normal	rotation	normal	≥24	II	P_1^2–P_3	Archbold and Thomas, 1985
Gypospirifer	plate	normal	rotation; JP	normal	22	I	C_2–P_1, P_2^2–P_3	Cooper and Grant, 1976a
Lepidospirifer	plate	normal	JP	normal	≥14	I	P_2^2	Cooper and Grant, 1976a
Spiriferella	plate	normal	rotation; JP	normal	11–17	I	C_2–P	Cooper and Grant, 1976a; Lee et al., 2019b
Timaniella	rod	normal	attenuation	normal	16–24	II	P_1^3–P_3^1	Lee et al., 2017, 2019b
Quiringites	plate	normal	rotation	normal	7–9	II	D_1^3–D_2^2	Schemm-Gregory, 2009
Intermedites	plate	normal	rotation	normal	≥13	II	D_2^1	Schemm-Gregory, 2010b
Rostrospirifer	plate	normal	rotation	normal	17	II	D_1^2–D_1^3	Schemm-Gregory, 2010b
Otospirifer	plate	normal	rotation	normal	>19	II	D_1^3	Schemm-Gregory, 2010b
Costispirifer		normal	JP	normal	≥14	I	D_1^2	Hall and Clarke, 1894; Schemm-Gregory, 2008
Leonispirifer	plate	normal	rotation	normal	18–20	II	D_1^3	Schemm-Gregory, 2010a
Thomasaria?	plate	normal	rotation	normal	2–3	II	D_3^1	Lü and Ma, 2017
Phricodothyris	plate	normal	rotation	normal	10	II	C–P	Jin and Sun, 1981

Ladjia, *Xiangia* Lü and Ma, 2017, *Elythyna* Rzhonsnitskaia, 1952, *Martiniopsis* Waagen, 1883, *Crassispirifer* Archbold and Thomas, 1985, *Timaniella* Barkhatova, 1968, *Quiringites* Struve, 1992, *Intermedites* Struve, 1995, *Rostrospirifer* Grabau, 1931, *Otospirifer* Hou and Xian, 1975, *Leonispirifer* Schemm-Gregory, 2010a, *Thomasaria* Stainbrook, 1945, and *Phricodothyris* George, 1932 (Table 2).

Similarly, the modified group can be divided into Type-III and Type-IV according to the curvature of the modified primary lamellae. Type-III is characterized by lateral-convex primary lamellae and appears in *Crurithyris* and *Weiningia* (Table 2; Fig. 5.3, 5.15). Type-IV, having medial-convex primary lamellae, is confined to *Attenuatella*, *Biconvexiella*, *Cruricella*, and *Orbicoelia* (Table 2; Fig. 5.10, 5.13). Spiral coils are developed in *Cruricella* and *Orbicoelia*, but are reduced in *Attenuatella* and *Biconvexiella*.

Distributions and significance of brachidium.—The distribution of the selected genera bearing different types of brachidium shows that more than one type of brachidium appears within the same superfamilies (Ambocoelioidea, Martinioidea, Spiriferoidea, Delthyridoidea; Fig. 6), families (Trigonotretidae, Spiriferellidae; Supplemental Table 1), and even subfamilies (Ambocoeliinae, Martiniinae, Neospiriferinae; Supplemental Table 1). Because the brachidium is a significant structure that reflects the phylogenetic relationship between and within the spire-bearing brachiopods (Copper and Gourvennec, 1996; Rong and Zhan, 1996; Gourvennec, 2000), spiriferides equipped with the same types of brachidium may share a close phylogenetic relationship. Some taxa may be rearranged under the current taxonomic ranks or reclassified under new taxonomic groupings, such as those in Atrypida (Copper, 2002) and Athyridida (Alvarez and Rong, 2002) in which the brachidial morphology serves as a diagnostic character within the suprageneric groups. For example, Type-II (*Ambocoelia*), Type-III (*Crurithyris*), and Type-IV (*Orbicoelia*, *Attenuatella*, *Biconvexiella*, *Cruricella*) are present in the Ambocoeliinae.

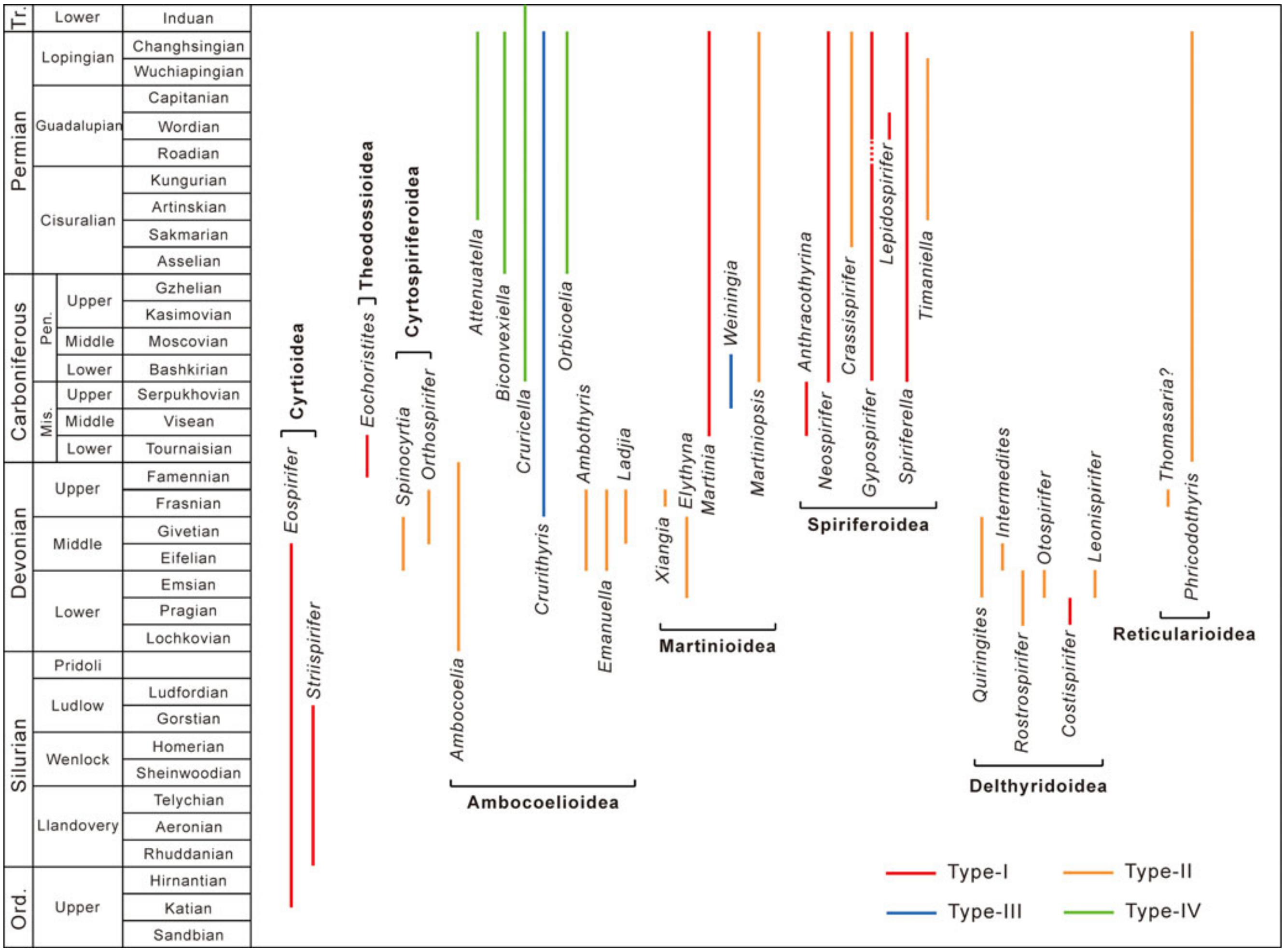

Figure 6. Stratigraphic ranges and types of brachidium of the selected taxa. Note that more than one type of brachidium appears in Ambocoelioidea, Martinioidea, Spiriferoidea, and Delthyridoidea, and that only one type in Cyrtioidea, Theodossioidea, Cyrtospiriferoidea, and Reticularioidea may result from limited taxa considered.

Zhang and Ma (2019) described several types of cardinal process and cruralium in the Ambocoeliidae and considered them as typical features of this family. These authors also mentioned that *Crurithyris* lacks dorsal adminicula and its cardinalia is identical to that of many other spiriferides belonging to the Martinioidea and Reticularioidea, implying that *Crurithyris* may not be an ambocoelioid. Having a similar cardinalia and shell morphology to that of *Crurithyris*, *Attenuatella*, *Biconvexiella*, *Curicella*, and *Orbicoelia* may also be excluded from the Ambocoeliidae and exhibit a different evolutionary lineage (Zhang and Ma, 2019). The different brachidia in *Attenuatella*, *Biconvexiella*, *Crurithyris*, *Curicella*, and *Orbicoelia* compared to *Ambocoelia* again bring the taxonomic positions of these taxa within the Ambocoeliidae into question. The Martiniinae is another noteworthy example for bearing Type-I (*Martinia*) and Type-III brachidia (*Weiningia*), which display significant differences from each other in terms of the configuration of the jugal processes and types of primary lamellae. However, it is difficult to determine whether the difference in brachidial morphology is of phylogenetic significance at the current time because the examined taxa only make up a small part of this order, even within the selected superfamilies.

Evolutionary relationship between brachidia.—The similarities between different types of brachidia, especially Type-I and Type-II, and Type-III and Type-IV, make it possible to investigate their evolutionary relationship. Type-I represents the oldest type of brachidium and first appeared in *Eospirifer praecursor* Rong, Zhan, and Han, 1994 in the late Katian of the Ordovician (Rong et al., 1994; Zhan et al., 2011, 2012). According to Rong and Zhan (1996), the morphologies of the crura and brachidium of *E. praecursor* (i.e., short crura, jugal processes, posterolaterally directed spiralia with few whorls) are similar to those of the early atrypide *Cyclospira* Hall and Clark, 1893, which bears ventrally arched crura, and small spiralia with few whorls and no jugum (Copper, 1986), indicate that *Eospirifer* may have a close phylogenetic relationship with early atrypides. Type-I did not undergo considerable change from the Late Ordovician through to the end of the Permian (Fig. 7). The lack of Type-I in the interval from the Givetian to the early Famennian of the Devonian may be the result of the limited taxa considered (Fig. 6).

With the first appearance at the beginning of the Devonian, Type-II, which existed until the end of the Permian (Figs. 6, 7), was likely derived from Type-I by loss of the jugal processes

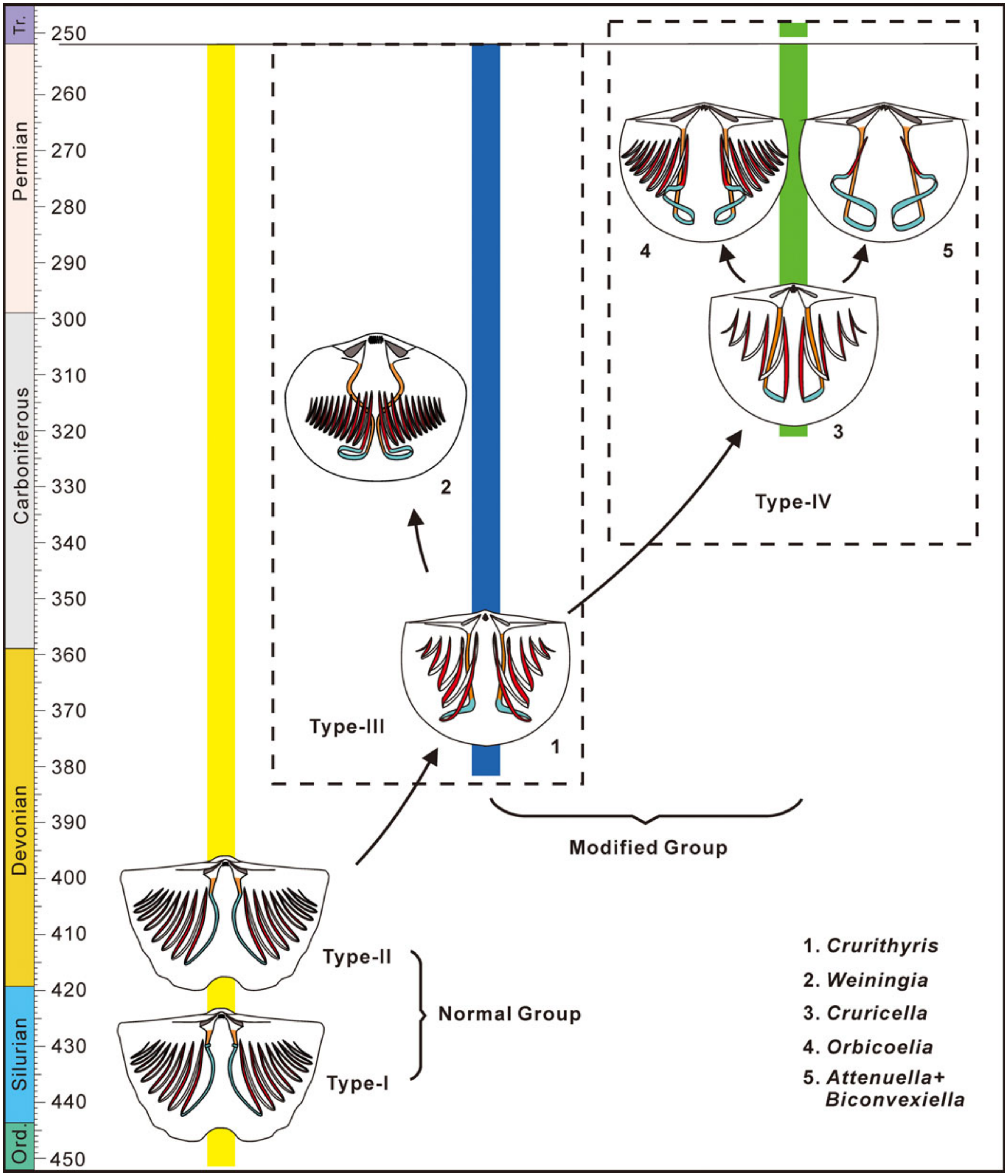

Figure 7. Speculative evolutionary pattern of brachidia in Order Spiriferida.

during the Late Ordovician to the beginning of the Devonian. In subsequent periods, Type-II may revert to Type-I by regaining the jugal processes if the jugal process development could occur independently in different superfamilies (Fig. 6). As a vestigial trace of the jugum in the ancestries of Spiriferida, the subdivision of the normal group into Type-I and Type-II is subjective merely based on the presence/absence of the jugal process, which is probably of very limited phylogenetic value.

The modified group exhibits more significant brachidial innovation. Type-III appears in *Crurithyris* and *Weiningia*, with the former ranging from the Late Devonian to the Permian and the latter restricted to the late Early Carboniferous (Fig. 6). Type-IV is found in *Attenuatella*, *Biconvexiella*, *Crurícella*, and *Orbicoelia*, among which *Crurícella* first appeared in the Late Carboniferous and existed until the Early Triassic, whereas the others are confined to the Permian (Fig. 6). Although some taxa bearing the same brachidial type are not phylogenetically related, the morphology and stratigraphic distribution of different brachidial types clearly show a temporal trend from the normal brachidia to the modified ones (Fig. 7), suggesting that the latter was derived from the former. Because the modified brachidia are closely associated with the prolongation of crura, it is necessary for Type-II to achieve two prerequisites before evolving the modified brachidia, namely elongation of the crura and enlargement of the first whorls of the spiralia. These features already appeared independently in some Middle Devonian ambocoeliides, such as the prolonged crura in *Echinocoelia* Cooper and Williams, 1935, and the disproportionately enlarged first whorls of spiralia in *Ladjia* sp. and "*Emanuella*" *meristoides* Meek, 1867 (Caldwell, 1968; Ma, 2009; Fig. 5.8, 5.9). *Crurithyris* is the oldest genus with the Type-III brachidium, which likely originated from Type-II by simple lateroventral bending of the primary lamellae. The brachidium of *Weiningia*, on the other hand, could have evolved from one morphologically similar to that of *Crurithyris* by developing the more complex lateral-convex primary lamellae. The similarity in brachidial morphology between *Crurithyris* and *Weiningia* does not indicate their phylogenetic relationship, but rather a similar ecological adaptation on the feeding mechanism.

Type-IV originated either from Type-II by evolving the medial-convex primary lamellae and placing them anteriorly to the spiral cones, or from Type-III similar to that in *Crurithyris* through the change of primary lamellae from lateral-convex type to medial-convex type only (Fig. 7). The latter seems more convincing because these genera bearing Type-IV brachidia are phylogenetically closely related to *Crurithyris*, and the brachidial morphology of *Crurícella* is very similar to that of *Crurithyris* except for the initial direction or course of the primary lamellae. Such morphological change can be achieved in the secretion and resorption processes controlled by the sheathed outer epithelium during growth of the brachidia (Williams et al., 1997b) to produce the simplest Type-IV brachidium, as in *Crurícella* from that in *Crurithyris*.

The complex medial-convex primary lamellae, appearing as S-shaped curvatures in *Attenuatella*, *Biconvexiella*, and *Orbicoelia*, were derived from those of *Crurícella* subsequently. In this case, the similarity in brachidial morphology among these ambocoeliines reflects not only a similar ecological adaptation on the feeding mechanism, but also their phylogenetic relationship. The brachidia in *Orbicoelia*, *Attenuatella*, and *Biconvexiella* represent two evolutionary lineages from *Crurícella*, with the spires maintained in *Orbicoelia* and reduced or lost in *Attenuatella* and *Biconvexiella* (Fig. 7).

The possible evolutionary lineage between different brachidia within Spiriferida may, in part, reflect the modification in the feeding system by improving the flexibility of the lophophores (through poorly developed/loss of jugal processes, loss of spiral coils) and a change in the mouth location (as shown by prolonged crura). In contrast to atrypides and athyridides, which have complex evolutionary modifications of the jugal structures (Alvarez and Rong, 2002; Copper, 2002; Guo et al., 2015), the jugal processes in Spiriferida exhibit a trend of stagnant development or complete loss. Although the function of the jugal structure in the lophophore remains uncertain, Copper (2002) inferred that the absence of the jugum in large atrypides of Siluro-Devonian age may suggest that a complete jugum was vulnerable and liable to breakage in the case of growing sizes of spiralia, while separate jugal processes allowed greater flexibility in the spiralia. This may suggest an analogous evolutionary trend of losing jugal processes in Spiriferida to improve the mobility and flexibility of the spiralia. As a vestigial feature, the presence/absence of the jugal process could be less important in improving the feeding system because Type-I and Type-II brachidia in the normal group are very similar in morphology.

On the other hand, Type-III and Type-IV brachidia are closely associated with prolongation of the crura, indicating not only a change in morphology of the brachidia but also a possible change in the position of the esophagus. The crura grow forward on either side of the esophagus to connect with the anterior body wall and posterior part of the lophophore on either side of the mouth in living brachiopods, therefore all processes so named in fossil rhynchonellides, terebratulides, and many spire-bearing brachiopods are thought to perform a similar function (Williams et al., 1997b). If so, the prolongation of crura in the modified group would indicate a displacement of the mouth to the anterior part of mantle cavity, accompanied by the forward extension of the esophagus along the dorsal mantle lobe (Fig. 8).

Modification of the brachidia (as in Type-III and Type-IV brachidia) may be fossil evidence of evolutionary change in the soft body of the brachiopod. Since many studies and experimental models strongly suggested that the feeding current systems in the fossil spire-bearing brachiopods with laterally tapered spiralia consisted of medially inhalant current and laterally exhalant currents (Manceñido and Gourvennec, 2008; Shiino et al., 2009; Shiino and Kuwazuru, 2011), the anterior-positioned mouth would get food particles quickly from the inhalant current at the anterior gape. The modified primary lamellae with the ciliated tentacles would serve as a pair of almost vertical, face-to-face, or semicircular loops to adjust or regulate the feeding currents delicately. Thus, Type-III and Type-IV brachidia represent an innovative modification of their feeding apparatus. As for the brachidia of *Attenuatella* and *Biconvexiella*, the loss of spiral coils probably reflects the presence of a flexible lophophore similar to that in the extant spirolophe-bearers, assuming that the lophophore was not restricted to this reduced brachidium. The brachidia of *Attenuatella* and *Biconvexiella* may represent an evolutionary trend towards mobile feeding organs without the support of spiralia. This unsupported lophophore may have extended out of the shell and captured food particles like the modern rhynchonellides *Notosaria nigricans* Sowerby, 1846 (Hoverd, 1985).

Conclusions

The variations of each component of brachidia in Spiriferida, namely the primary lamellae and the subsequent spires, are similar to the degree of variation in the other spire-bearers. Based on

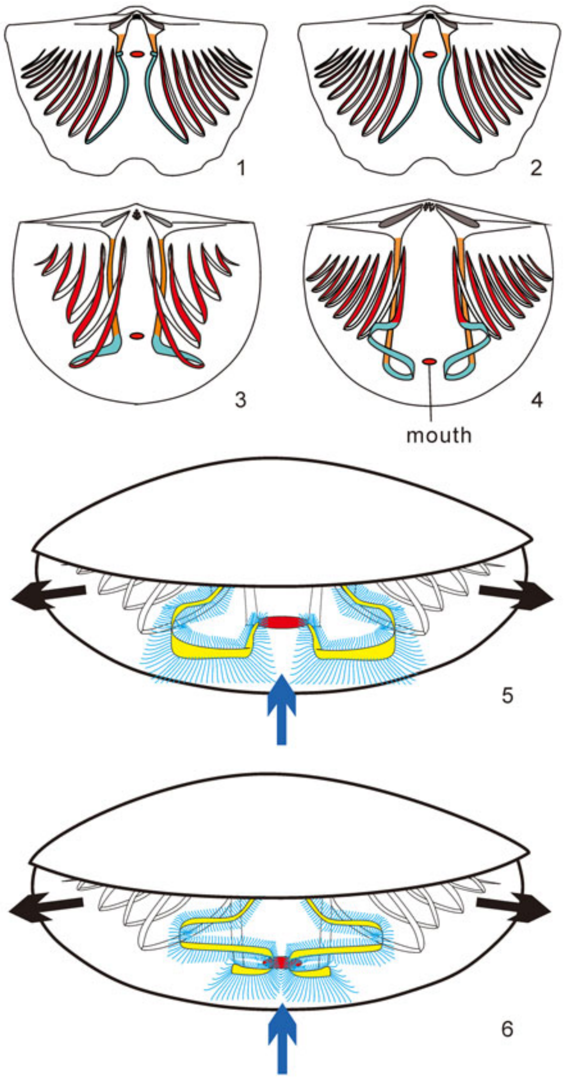

Figure 8. Relationship between the supposed mouth position and brachidial types in the spiriferides. (**1, 2**) Mouth opened in body wall posterior to the mantle cavity in taxa with normal brachidium (Type-I and Type-II); (**3, 4**) mouth opened at anterior part of the mantle cavity through the dorsal mantle lobe in taxa with modified brachidium (Type-III and Type-IV); (**5, 6**) restoration of the lophophore on the modified primary lamellae (lateral-convex and medial-convex) of the spiralia in relation to the feeding current system in modified group.

the configuration of the jugal processes (presence/absence), spiral coils (presence/absence), and types of primary lamellae (normal/lateral-convex/medial-convex), two groups composed of four types of brachidium are recognized. The normal group dominates in the studied taxa and is featured by normal primary lamellae and the presence of spiral coils, whereas the modified group occurs in a small number of taxa and is characterized by modified primary lamellae and the absence of jugal processes. In terms of the configuration of the jugal processes, the normal group is divided into Type-I (with jugal processes) and Type-II (without jugal processes). The modified group also consists of two types of brachidium, characterized by the presence of lateral-convex primary lamellae in Type-III and medial-convex ones in Type-IV.

The distributions of these types of brachidia within Spiriferida are variable, with more than one type present within the same suprageneric groups. Although it is worth considering the taxonomic significance of the brachidium within Spiriferida, given that this structure is regarded as an important diagnostic characteristic in the other spire-bearing brachiopods, it is challenging to incorporate a phylogenetic analysis to discuss this issue in detail due to limited taxa. Therefore, more detailed brachidial information in different taxa is needed. In addition, the similarities between different types of brachidia also make it possible to investigate their phylogenetic relationships. Type-II was probably derived from Type-I through loss of the jugal processes, and it could conversely give rise to Type-I by re-evolving the jugal processes in subsequent periods. Type-III may have evolved from Type-II through forming lateral-convex primary lamellae. The brachidium of *Cruricella*, one of the Type-IV brachidia, possibly originated from the brachidium of *Crurithyris*, one of the Type-III brachidia, through changing the orientation of primary lamellae during development. This simplest brachidium among Type-IV evolved into more complex forms in *Orbicoelia* (with spires) and *Attenuatella* and *Biconvexiella* (without spires).

The modified brachidia, closely associated with the prolongation of crura, represents an innovative modification of their feeding apparatus, possibly corresponding to the mouth shifting towards the anterior. The anterior-positioned mouth could help the creatures ingest food particles more rapidly and efficiently from the inhalant current at the anterior gape, and the modified primary lamellae could adjust/regulate the feeding currents and gather the food particles through the ciliated tentacles on these structures. The loss of the spires in *Attenuatella* and *Biconvexiella* probably suggests the evolution of a flexible lophophore without the support of spiralia, similar to extant spirolophe-bearing taxa. This unsupported lophophore could have extended out of the shell and captured food particles.

Acknowledgments

The authors are grateful to M.A. Torres-Martínez and S. Lee for their careful reviews and constructive comments, which greatly improved the manuscript. The authors also thank A. Baliński for improving the manuscript. This research was supported by a National Natural Science Foundation of China (NSFC) grant (No. 41772015).

Accessibility of supplemental data

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2fqz612n5.

References

Ager, D.V., and Riggs, E.A., 1964, The internal anatomy, shell growth and asymmetry of a Devonian spiriferid: Journal of Paleontology, v. 38, p. 749–760.

Alvarez, F., and Rong, J.Y., 2002, Athyridida, *in* Kaesler, R.L., ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda Revised, Volume 4: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America and University of Kansas Press, p. 1475–1583.

Archbold, N.W., and Thomas, G.A., 1985, New genera of Western Australian Permian Spiriferidae (Brachiopoda): Alcheringa, v. 9, p. 269–292.

Archbold, N.W., and Thomas, G.A., 1986, Permian Ingelarellidae (Brachiopoda) from Western Australia and Argentina: Journal of paleontology, v. 60, p. 581–605.

Armstrong, J., 1968, The unusual brachial skeleton of *Attenuatella convexa* sp. nov. (Brachiopoda): Palaeontology, v. 11, p. 783–792.

Barkhatova, V.P., 1968, Novye vidy pozdnepaleozoiskikh khorridonii severnogo Timana, *in* Markowskii, B.P., ed., Novye vidy drevnikh rastenii i bespozvonochnykh SSSR: Moscow, Nedra, p. 98–100, 160–167. [in Russian]

Boucot, A.J., Johnson, J.G., Pitrat, C.W., and Staton, R.D., 1965, Spiriferida, *in* Moore, R.C., ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda, Volume 2: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America and University of Kansas Press, p. H632–H728.

Brown, I.A., 1953, *Martiniopsis* Waagen from the Salt Range, India: Journal and Proceedings of the Royal Society of New South Wales, v. 86, p. 100–107.

Brunton, C.H.C., 1984, Silicified brachiopods from the Viséan of County Fermanagh, Ireland (III). Rhynchonellids, spiriferids and terebratulids: Bulletin of the British Museum (Natural History), Geology, v. 38, p. 27–130.

Brunton, C.H.C., and Champion, C., 1974, A Lower Carboniferous brachiopod fauna from the Manifold Valley, Staffordshire: Palaeontology, v. 17, p. 107–111.

Caldwell, W.G.E., 1968, Ambocoeliid brachiopods from the Middle Devonian rocks of northern Canada, *in* Oswald, D.H., ed., International Symposium on the Devonian System. Alberta, Alberta Society of Petroleum Geologists Calgary, p. 601–616.

Campbell, K.S.W., 1961, New species of the Permian spiriferoids *Ingelarella* and *Notospirifer* from Queensland and their stratigraphic implications: Palaeontographica, Abteilung A, v. 117, p. 159–192.

Carter, J.L., 1972, Early Mississippian brachiopods from the Gilmore City Limestone of Iowa: Journal of Paleontology, v. 46, p. 473–491.

Carter, J.L., 1974, New genera of spiriferid and brachythyridid brachiopods: Journal of Paleontology, v. 48, p. 674–696.

Carter, J.L., 1985, The Lower Mississippian brachiopod genus *Punctothyris* Hyde is not endopunctate: Annals of Carnegie Museum, v. 54, p. 375–391.

Carter, J.L., and Johnson, J.G., 2006, Spiriferinida, *in* Kaesler, R.L., ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda Revised, Volume 5: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America and University of Kansas Press, p. 1877–1937.

Carter, J.L., Johnson, J.G., Gourvennec, R., and Hou, H.F., 1994, A revised classification of the spiriferid brachiopods: Annals of Carnegie Museum, v. 63, p. 327–374.

Carter, J.L., Johnson, J.G., Gourvennec, R., and Hou, H.F., 2006, Spiriferida, *in* Kaesler, R.L., ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda Revised, Volume 5: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America and University of Kansas Press, p. 1689–1876.

Chen, Z.Q., Kaiho, K., George, A.D., and Tong, J.N., 2006, Survival brachiopod faunas of the end-Permian mass extinction from the southern Alps (Italy) and South China: Geological Magazine, v. 143, p. 301–327.

Chernyshev, T.N., 1902, Die obercarbonischen Brachiopoden des Ural und des Timan: Mémoires du Comité Géologique, v. 16, p. 1–749. [in Russian and German]

Chu, S., 1933, Corals and Brachiopoda of the Kinling Limestone: National Research Institute of Geology, Academia Sinica, Monographs (Nanking), Ser. A, v. 2, 73 p.

Cloud, P.E., Jr, 1944, Permian brachiopods, *in* King, R.E., Dunbar, C.O., Cloud, P.E., Jr, and Miller, A.K., eds., Geology and Paleontology of the Permian Area Northwest of Las Delicias, Southwestern Coahuila, Mexico: Geological Society of America Special Papers, v. 52, p. 49–69.

Cooper, G.A., 1942, New genera of North American brachiopods: Journal of the Washington Academy of Sciences, v. 32, p. 228–235.

Cooper, G.A., and Dutro, J.T., Jr, 1982, Devonian brachiopods of New Mexico: Bulletins of American Paleontology, v. 82–83, p. 1–215.

Cooper, G.A., and Grant, R.E., 1969, New Permian brachiopods of west Texas I: Smithsonian Contributions to Paleobiology, v. 1, p. 1–20.

Cooper, G.A., and Grant, R.E., 1976a, Permian brachiopods of west Texas IV: Smithsonian Contributions to Paleobiology, v. 21, p. 1923–2607.

Cooper, G.A., and Grant, R.E., 1976b, Permian Brachiopods of west Texas V: Smithsonian Contributions to Paleobiology, v. 24, p. 2609–3159.

Cooper, G.A., and Muir-Wood, H.M., 1951, Brachiopod homonyms: Journal of the Washington Academy of Sciences, v. 41, p. 195–196.

Cooper, G.A., and Williams, J.S., 1935, Tully Formation of New York: Geological Society of America Bulletin, v. 46, p. 781–868.

Copper, P., 1986, Evolution of the earliest smooth spire-bearing atrypoids (Brachiopoda: Lissatrypidae, Ordovician–Silurian): Palaeontology, v. 29, p. 827–866.

Copper, P., 2002, Atrypida, *in* Kaesler, R.L., ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda Revised, Volume 4: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America and University of Kansas Press, p. H1377–H1474.

Copper, P., and Gourvennec, R., 1996, Evolution of the spire-bearing brachiopods (Ordovician–Jurassic), *in* Copper, P., and Jin, J.S., eds., Brachiopods: Rotterdam, A.A. Balkema, p. 81–88.

Davidson, T., 1882, Supplement to the British Devonian Brachiopoda: Palaeontographical Society Monographs, v. 5, 134 p.

Emig, C.C., 1992, Functional disposition of the lophophore in living Brachiopoda: Lethaia, v. 25, p. 291–302.

Fleming, J., 1828, A History of British Animals, Exhibiting the Descriptive Characters and Systematical Arrangement of the Genera and Species of Quadrupeds, Birds, Reptiles, Fishes, Mollusca, and Radiata of the United Kingdom: Edinburgh and London, Bell and Bradfute and James Duncan, 565 p.

Frederiks, G.N., 1916, Paleontologicheskiya zametki. 2. O Nekotorykh verkhne-Paleozoiskikh brakhiopodakh Evrazii: Mémoires du Comité Géologique (new series), v. 156, p. 1–87. [in Russian]

Frederiks, G.N., 1924, Paleontologitcheskie ztoudy. 2: O verkhne kamennougolnykh spiriferidakh Ourala: Izvestiya geologicheskogo Komiteta, v. 38, p. 295–324. [in Russian]

George, T.N., 1931, *Ambocoelia* Hall and certain similar British Spiriferidae: Quarterly Journal of the Geological Society, v. 87, p. 30–62.

George, T.N., 1932, The British Carboniferous reticulate Spiriferidae: Quarterly Journal of the Geological Society of London, v. 88, p. 516–575.

Goldman, D., and Mitchell, C.E., 1990, Morphology, systematics, and evolution of Middle Devonian Ambocoeliidae (Brachiopoda), western New York: Journal of Paleontology, v. 64, p. 79–99.

Gourvennec, R., 2000, The evolution, radiation and biogeography of early spiriferid brachiopods: Records of the Western Australian Museum Supplement, v. 58, p. 335–347.

Grabau, A.W., 1923–1924, Stratigraphy of China. Part I, Palaeozoic and Older: Peking, Geological Survey of China, 528 p.

Grabau, A.W., 1931, Devonian Brachiopoda of China, I: Devonian Brachiopoda from Yunnan and other districts in South China: Palaeontologia Sinica, Series B, v. 3, p. 1–545.

Grant, R.E., 1976, Permian brachiopods from southern Thailand: Memoir of the Paleontological Society, v. 9, p. 1–269.

Guo, W., Sun, Y.L., and Baliński A., 2015, Parallel evolution of jugal structures in Devonian athyridide brachiopods: Palaeontology, v. 58, p. 171–182.

Hall, J., 1860, Observations of the genus *Ambocoelia*: Thirteenth Annual Report of the Regents of the University on the condition of the State Cabinet of Natural History, p. 71–72.

Hall, J., and Clarke, J.M., 1893, An introduction to the study of the genera of Palaeozoic Brachiopoda. II. Brachiopoda Articulata (continued): New York Geological Survey, Palaeontology, v. 8, 317 p.

Hall, J., and Clarke, J.M., 1894, An introduction to the study of the Brachiopoda, intended as a handbook for the use of students, Part II. New York State Geologist, Annual Report for 1893, v. 13, p. 751–943.

Havlíček, V., 1971, Non-costate and weakly costate Spiriferidina (Brachiopoda) in the Silurian and Lower Devonian of Bohemia: Sborník geologickýchvěd, Paleontologie, v. 17, p. 7–34.

Hou, H.F., and Xian, S.Y., 1975, The Lower and Middle Devonian brachiopods from Guangxi and Guizhou: Professional Papers of Stratigraphy and Palaeontology, v. 1, p. 1–85. [in Chinese]

Hoverd, W.A., 1985, Histological and ultrastructural observations of the lophophore and larvae of the brachiopod, *Notosaria nigricans* (Sowerby 1846): Journal of Natural History, v. 19, p. 831–850.

Ivanova, E.A., 1972, Main features of spiriferid evolution (Brachiopoda): Paleontologicheskii Zhurnal, v. 3, p. 28–42. [in Russian]

James, M.A., Ansell, A.D., Collins, M.J., Curry, G.B., Peck, L.S., and Rhodes, M.C., 1992, Biology of living brachiopods: Advances in Marine Biology, v. 28, p. 175–387.

Jin, Y.G., 1961, Additional brachiopods from the Kinling Formation of the lower Yangtze district. Acta Palaeontologica Sinica, v. 9, p. 272–290. [in Chinese]

Jin, Y.G., and Liao, Z.T., 1974. Brachiopoda (Carboniferous), *in* Nanjing Institute of Geology and Palaeontology, Academia Sinica, ed., A Handbook of the Stratigraphy and Palaeontology in Southwest China: Beijing, Science Press, p. 275–283. [in Chinese]

Jin, Y.G., and Sun, D.L., 1981, Paleozoic brachiopod fauna in Tibet, *in* Nanjing Institute of Geology and Palaeontology, Academia Sinica, ed., Paleontological Atlas of Tibet (3): Beijing, Science Press, p. 127–176. [in Chinese]

Lee, S., Shi, G.R., Park, T.Y.S., Oh, J.R., Mii, H.S., and Lee, M., 2017, Virtual palaeontology: the effects of mineral composition and texture of fossil shell and hosting rock on the quality of X-ray microtomography (XMT) outcomes using Palaeozoic brachiopods: Palaeontologia Electronica, v. 20, p. 1–25. https://doi.org/10.26879/753.

Lee, S., Shi, G.R., Jung, J., and Kim, N.K., 2019a, Discovery of ventrally directed spiralia in a Permian spiriferellid brachiopod and implications for its feeding system: Lethaia, v. 52, p. 513–522.

Lee, S., Shi, G.R., Woo, J., Park, T.Y.S., Oh, J.R., Kim, N.K., Nakrem, H.A., and Tazawa, J.I., 2019b, Permian spiriferellid brachiopods from northern Pangaea: taxonomy, biostratigraphy, macroevolution and implications for palaeoenvironmental and palaeobiogeographical reconstructions: Journal of Systematic Palaeontology, v. 17, p. 1871–1925. https://doi.org/10.1080/14772019.2019.1570569.

Legrand-Blain, M., 1984, Étude paléontologique, *in* Legrand-Blain, M., Devolvé, J.J., and Perret, M.F., ed., Les brachiopods Carbonifères des Pyrénées Centrales Françaises. 2: Étude des Orthida et des Spiriferida; Biostratigraphie, Paléoécologie, Paléobiogéographie. Geobios, v. 17, p. 297–325.

Li, R.Y., and Jones, B., 2007, Brachiopods from Bird Fiord Formation (Devonian) of Arctic Canada: Canadian Journal of Earth Sciences, v. 44, p. 1291–1311.

Lü, D., and Ma, X.P., 2017, Small-sized brachiopods from the Upper Frasnian (Devonian) of central Hunan, China: Palaeoworld, v. 26, p. 456–478.

Ma, X.P., 2009, Spiriferide brachiopods from the Frasnian (Devonian) of the Dushan area, southern Guizhou, China: Acta Palaeontologica Sinica, v. 48, p. 611–627.

Manceñido, M.O., and Gourvennec, R., 2008, A reappraisal of feeding current systems inferred for spire-bearing brachiopods: Earth and Environmental Science Transactions of the Royal Society of Edinburgh, v. 98, p. 345–356.

M'Coy, F., 1844, A Synopsis of the Characters of the Carboniferous Limestone Fossils of Ireland: Dublin, Dublin University Press, 207 p.

Meek, F.B., 1867, Remarks on the geology of the valley of Mackenzie River, with figures and descriptions of fossils from that region, in the Museum of the Smithsonian Institution, chiefly collected by the late Robert Kennicott, Esq: Transactions of the Chicago Academy of Science, v. 1, p. 61–113.

Muir-Wood, H.M., 1965, Mesozoic and Cenozoic Terebratulidina, *in* Moore, R.C., ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda, Volume 2: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America and University of Kansas Press, p. H762–H816.

Muir-Wood, H.M., Elliott, G.F., and Kotora, H., 1965, Mesozoic and Cenozoic Terebratellidina, *in* Moore, R.C., ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda, Volume 2: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America and University of Kansas Press, p. H816–H857.

Pitrat, C.W., 1975, *Orthospirifer* new genus of Devonian spinocyrtiid brachiopods: Journal of Paleontology, v. 49, p. 387–394.

Pitrat, C.W., 1977, Spiriferid brachiopods from the Traverse Group of Michigan: *Orthospirifer*: Journal of Paleontology, v. 51, p. 330–342.

Rong, J.Y., and Yang, X.C., 1978, Silurian spiriferoids from southwest China with special reference to their stratigraphic significance: Acta Palaeontologica Sinica, v. 17, p. 357–384. [in Chinese with English summary]

Rong, J.Y., and Zhan, R.B., 1996, Brachidia of Late Ordovician and Silurian eospiriferines (Brachiopoda) and the origin of the spiriferides: Palaeontology, v. 39, p. 941–978.

Rong, J.Y., Zhan, R.B., and Han, N.R., 1994, The oldest known *Eospirifer* (Brachiopoda) in the Changwu Formation (Late Ordovician) of western Zhejiang, East China, with a review of the earliest spiriferoids: Journal of Paleontology, v. 68, p. 763–776.

Rudwick, M.J.S., 1962, Filter-feeding mechanisms in some brachiopods from New Zealand: Zoological Journal of the Linnean Society, v. 44, p. 592–615.

Rudwick, M.J.S., 1970, Living and Fossil Brachiopods: London, Hutchinson and Company, 199 p.

Rzhonsnitskaya, M.A., 1952, Spiriferidy Devonskikh otlojenii okrain Kouznetskogo Basseina: Trudy VSEGEI, Moscow, Gosgeolizdat, 231 p. [in Russian]

Schemm-Gregory, M., 2008, New interpretations of the phylogeny and taxonomy of delthyridoid spiriferids (Brachiopoda, Lower and Middle Devonian): Bulletin of Geosciences, v. 83, p. 401–448.

Schemm-Gregory, M., 2009, On the genus *Quiringites* Struve, 1992 (Brachiopoda, Middle Devonian): Bulletin of the Peabody Museum of Natural History, v. 50, p. 3–21.

Schemm-Gregory, M., 2010a, *Leonispirifer leonensis* gen. et sp. nov., a rare new delthyridoid spiriferid brachiopod from northern Spain (Brachiopoda, Lower Devonian): Paläontologische Zeitschrift, v. 84, p. 345–364.

Schemm-Gregory, M., 2010b, *Intermedites* Struve, 1995 (Brachiopoda, Middle Devonian)—discovery of a south Chinese immigrant in Europe and North Africa: Acta Palaeontologica Sinica, v. 49, p. 425–438.

Schuchert, C., 1913, Class 2. Brachiopoda, *in* von Zittel, K.A., ed., Text-book of Palaeontology, Part 1, 2nd edition: London, MacMillan and Company Limited, v. 1 p. 355–420.

Shen, S.Z., and Clapham, M.E., 2009, Wuchiapingian (Lopingian, Late Permian) brachiopods from the Episkopi Formation of Hydra Island, Greece: Palaeontology, v. 52, p. 713–743.

Shi, G.R., Chen, Z.Q., Lee, S., and Zhan, L.P., 2016, Early Carboniferous spiriferoid brachiopods from the Qaidam Basin, Northwest China: taxonomy, biostratigraphy and biogeography: Palaeoworld, v. 25, p. 581–599.

Shiino, Y., and Kuwazuru, O., 2011. Theoretical approach to the functional optimisation of spiriferide brachiopod shell: optimum morphology of sulcus: Journal of Theoretical Biology, v. 276, p. 192–198.

Shiino, Y., Kuwazuru, O., and Yoshikawa, N., 2009, Computational fluid dynamics simulations on a Devonian spiriferid *Paraspirifer bownockeri* (Brachiopoda): generating mechanism of passive feeding flows: Journal of Theoretical Biology, v. 259, p. 132–141.

Sowerby, G.B., 1846, Descriptions of thirteen new species of brachiopods: Proceedings of the Zoological Society of London, v. 14, p. 91–95.

Sowerby, J.de C., 1823–1846, The Mineral Conchology of Great Britain; or coloured figures and descriptions of those remains of testaceous animals or shells, which have been preserved at various times and depths in the earth: London, Benjamin Meredith, v. 5–7.

Stainbrook, M.A., 1945, Brachiopoda of the Independence Shale of Iowa: Memoir of Geological Society of America, v. 14, p. 1–74.

Stehli, F.G., 1954, Lower Leonardian Brachiopoda of the Sierra Diablo: Bulletin of the American Museum of Natural History, v. 105, p. 257–358.

Strathmann, R.R., 2005, Ciliary sieving and active ciliary response in capture of particles by suspension-feeding brachiopod larvae: Acta Zoologica, v. 86, p. 41–54. https://doi.org/10.1111/j.1463-6395.2006.00224.x.

Struve, W., 1992, Neues zur stratigraphie und fauna des rhenotypen Mittel-Devon: Senckenbergiana lethaea, v. 71, p. 503–624.

Struve, W., 1995, Die Riesen-Phacopiden aus dem Maïder, SE-marokkanische Prä-Sahara: Senckenbergiana lethaea, v. 75, p. 77–129.

Sun, Y.L., and Baliński, A., 2011, Silicified Mississippian brachiopods from Muhua, southern China: rhynchonellides, athyridides, spiriferides, spiriferinides, and terebratulides: Acta Palaeontologica Polonica, v. 56, p. 793–842.

Tan, Z.X., 1987, Chapter 1 Stratigraphy, Chapter 2 Brachiopoda. *in* Tan, Z.X., Dong, Z.C., Jin, Y.L., Li, S.Q., and Yang, Y.C., eds., The Late Devonian and Early Carboniferous Strata and Palaeobiocoenosis of Hunan: Beijing, Geological Publishing House, p. 2–65, 111–133. [in Chinese with English summary]

Veevers, J.J., 1959, Devonian brachiopods from the Fitzroy Basin, Western Australia: Australia, Bureau of Mineral Resources, Geology and Geophysics, Bulletin 45, 220 p.

Waagen, W.H., 1883, Salt Range Fossils. I. *Productus*-Limestone Fossils: Brachiopoda: Geological Survey of India, Memoir, Palaeontologia Indica, Series 13, v. 4, p. 391–546.

Wang, Y., 1956, New species of brachiopods (2): Acta Palaeontologica Sinica, v. 4, p. 387–407. [in Chinese]

Waterhouse, J.B., 1964, Permian brachiopods of New Zealand: New Zealand Geological Survey, Paleontological Bulletin, v. 35, p. 1–287.

Waterhouse, J.B., 1968, The classification and descriptions of Permian Spiriferida (Brachiopoda) from New Zealand: Palaeontographica, Abteilung A, v. 129, p. 1–94.

Waterhouse, J.B., 1983, New Permian invertebrate genera from the east Australian segment of Gondwana: Bulletin of Indian Geologists' Association, v. 16, p. 153–158.

Waterhouse, J.B., 1998, Ingelarelloidea (Spiriferida: Brahiopoda) from Australia and New Zealand, and reclassification of Ingelarellidae and Notospiriferidae: Earthwise, v. 1, p. 1–48.

Waterhouse, J.B., and Piyasin, S., 1970, Mid-Permian brachiopods from Khao Phrik, Thailand: Palaeontographica, Abteilung A, v. 135, p. 83–197.

Williams, A., and Brunton, C.H.C., 1997, Morphological and anatomical terms applied to brachiopods, *in* Kaesler, R.L., ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda Revised, Volume 1: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America and University of Kansas Press, p. 423–440.

Williams, A., James, M.A., Emig, C.C., Mackay, S., and Rhodes, M.C., 1997a, Anatomy, *in* Kaesler, R.L., ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda Revised, Volume 1: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America and University of Kansas Press, p. 7–188.

Williams, A., Brunton, C.H.C., and MacKinnon, D.I., 1997b, Morphology, *in* Kaesler, R.L., ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda Revised, Volume 1: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America and University of Kansas Press, p. 321–422.

Yang, D.L., Ni, S.Z., Chang, M.L., and Zhao, R.X., 1977, Brachiopoda, *in* Institute of Geological Science of Hubei Province, ed., Paleontological Atlas of Central-South China (2): Beijing, Geological Publishing House, p. 306–470. [in Chinese]

Yang, S.P., 1964, Brachiopods from the Tournaisian of the Carboniferous in Southeast Guizhou, China: Acta Palaeontologica Sinica, v. 1, p. 82–109. [in Chinese]

Yuan, Z.W., Sun, Y.L., Shen, B., Xing, C.C., Liu, W., Yang, R.Y., Qin, S.J., and Baliński, A., 2019, An in situ preserved early Carboniferous (Serpukhovian) brachiopod community in Southern Guizhou, China: Rivista Italiana di Paleontologia e Stratigrafia, v. 125, p. 689–710.

Zhan, R.B., Liang, Y., and Meng, L.K., 2011, On the macroevolution of *Eospirifer* Schuchert, 1913 (Spiriferida, Brachiopoda), *in* Gutiérrez-Marco, J.C., Rábano, I., and García-Bellido D., eds., Ordovician of the World: Madrid, Cuadernos del Museo Geominero, 14. Instituto Geológico y Minero de España, p. 633–648.

Zhan, R.B., Jin, J.S., Liang, Y., and Meng, L.K., 2012, Evolution and paleogeography of *Eospirifer* (Spiriferida, Brachiopoda) in Late Ordovician and Silurian: Science China Earth Sciences, v. 55, p. 1427–1444.

Zhang, M.Q., 2016, Middle-Upper Devonian Boundary: Geochemical Characteristics, Brachiopod Fauna and their Stratigraphic Significance [Ph.D. dissertation]: Beijing, Peking University, 116 p. [in Chinese with English abstract]

Zhang, M.Q., and Ma, X.P., 2019, Origination and diversification of Devonian ambocoelioid brachiopods in South China: Palaeobiodiversity and Palaeoenvironments, v. 99, p. 63–90.

Accepted: 20 November 2020