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湖南上泥盆统(弗拉阶)几种石松类孢子叶球新类型*

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提要 具有孢子叶球的石松类始现于中泥盆世吉维特期,繁盛于晚泥盆世法门期,但其弗拉期化石记录较为缺乏。基于湖南长沙附近弗拉阶云麓宫组的材料,本文描述了三种石松类孢子叶球未定类型。其中一类孢子叶球具有独特的孢子叶形态和排列方式:其孢子叶呈交互假轮生排列,每轮四枚;叶片呈斜方形,顶端具线形叶尖。另两种石松类叶球未定类型分别以无柄的孢子叶和二分叉的叶球为特征。本文复原了第一类叶球的三维形态,就压型保存的石松类孢子叶球化石的埋藏学进行了讨论,并将所研究的三种石松类孢子叶球与相关植物进行对比,增进了对弗拉期石松类繁殖器官多样性的认识。

关键词 石松植物 孢子叶球 埋藏学 弗拉期 植物化石

NEW LYCOPSIDS STROBILUS WITH DIVERGENT MORPHOLOGIES FROM THE UPPER DEVONIAN (FRASNIAN) OF HUNAN, CHINA

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Abstract Lycopsid with strobili first occurred in the Givetian and were abundant in the Famennian of the Devonian, while their fossil record in the Frasnian is insufficient. Based on specimens from the Frasnian Yunlugong Formation at a location near Changsha City, Hunan Province, China, we describe three undetermined lycopsid strobili showing divergent morphologies despite the limited material. One type of these strobili displays unique morphological traits, including the slender strobili bearing sporophylls in alternate pseudowhorls of four, and the sporophylls with linear distal tips and rhombic laminae. The other two types of undetermined strobili are characterized by sessile sporophylls and bifurcate strobilar axes, respectively. The first type mentioned above is reconstructed and discussed within a taphonomic context of compression fossils of strobili. The present materials are compared with related taxa, and add to the diversity of the reproductive organs of Frasnian lycopsids.

Key words Lycopsids, strobili, taphonomy, Frasnian, plant fossils

1 INTRODUCTION

Lycopsids represent one of the earliest diverging lineages of vascular land plants, which probably originated in the late Silurian and first radiated in the Early Devonian (Stewart and Rothwell, 1993; Taylor *et al.*, 2009; Hao and Xue, 2013).

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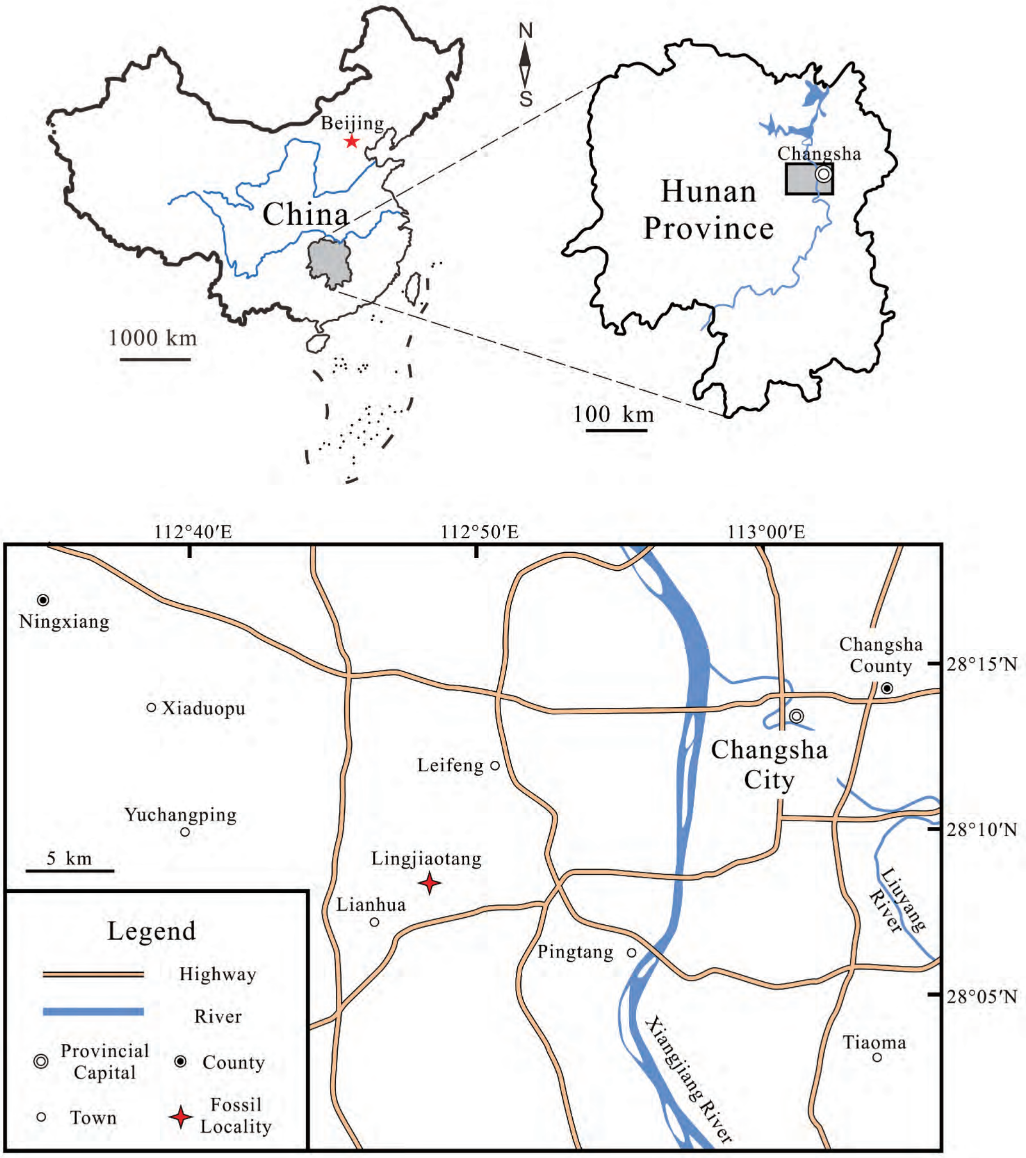
Within lycopsids, the sporangia are either born laterally on the axes in the drepanophycaleans, the basalmost group (e. g. Xue, 2013; Xu *et al.*, 2013; Matsunaga and Tomescu, 2017); or attached to the adaxial surface or the axil of sporophylls in other later groups (Gensel and Berry, 2001). Sporophylls display two major distribution patterns among younger lycopsid clades: some are scattered along axes to form intercalary fertile zones (Wang and Berry, 2003; Zhang *et al.*, 2016), while most are aggregated into compact terminal strobili. Lycopsid strobili first appeared in the late Middle Devonian (Senkevitsch *et al.*, 1993; Cai and Chen, 1996; Hao *et al.*, 2007), and showed great diversity in the Late Devonian Famennian (e. g. Meng *et al.*, 2013, 2015; Wang *et al.*, 2014, 2017; Evreïnoff *et al.*, 2017; Gess and Prestianni, 2018). However, the fossil records of lycopsids, especially the fertile parts, are rare in the Frasnian deposits, resulting in an incomplete understanding of lycopsid evolution. In this paper, three undetermined lycopsid strobili with divergent morphologies are reported from the Frasnian of Hunan Province, China (Text-fig. 1). This paper also presents a morphological comparison with other related taxa, and a consideration about the taphonomy of strobili preserved as compression fossils. In addition, the evolutionary significance of these lycopsids is addressed.

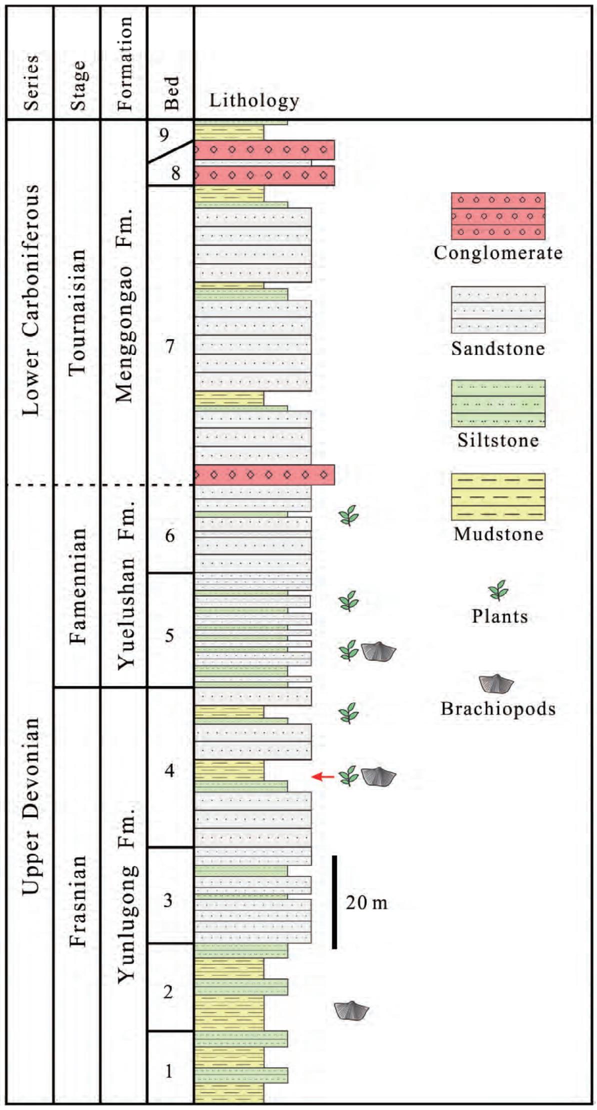


Text-figure 1 Map showing the fossil locality (Lingjiaotang section, near Lianhua Town, Changsha City, Hunan Province, China).

2　MATERIAL AND METHODS

About twenty specimens were obtained at Lingjiaotang section along the canal of a reservoir near Lianhua Town, Wangcheng District of Changsha City, Hunan Province, China (Text-fig. 1). The GPS location is 28°8′9.47″N and 112°48′15.16″E. The strata exposed at Lingjiaotang section are ca. 210 m thick and include three parts in ascending order (Text-fig. 2): the lower part, composed of quartzose sandstone with interbedded silty mudstone and containing brachiopod fossils including *Cyrtospirifer* sp., *Atrypa shetienchiaoensis*, *A. douvilii* and *Spinatrypa* sp., was regarded as the Frasnian Yunlugong Formation; the middle part consists of quartzose sandstone with intercalated mudstone, and was identified as Famennian Yuelushan Formation based on a brachiopod assemblage rich in *Yunnanella*; the disconformably overlying upper part, Tournaisian Menggongao Formation, is dominated by pebbly sandstone and hematite (Zhao *et al*., 1978; Tan and Wang, 1983; Wang, 2007).

The present specimens are preserved in an interlayer of silty mudstone in the upper part of the Yunlugong Formation (bed 4 in Text-fig. 2, red arrow), together with plant fossils of *Sublepidodendron* and *Leptophloeum* and brachiopods *Cyrtospirifer*, *Atrypa* and *Spinatrypa*. *Tenuisa frasniana*, a euphyllophyte plant, occurs in the adjacent overlying layers at the upper part of the Yunlugong Formation (Wang, 2007). The present plants are preserved as impression and compression in brown color, showing high contrast with the grayish-yellow rock matrix. Steel needles were used to reveal morphological details of the specimens. Digital cameras and stereoscope were used for photographing. All the specimens are housed at School of Earth and Space Sciences, Peking University, China.



Text-figure 2　Stratigraphic column of the Upper Devonian-Lower Carboniferous at the Lingjiaotang section. Modified from Tan and Wang (1983). Red arrow indicating the bed containing plant fossils studied in this paper.

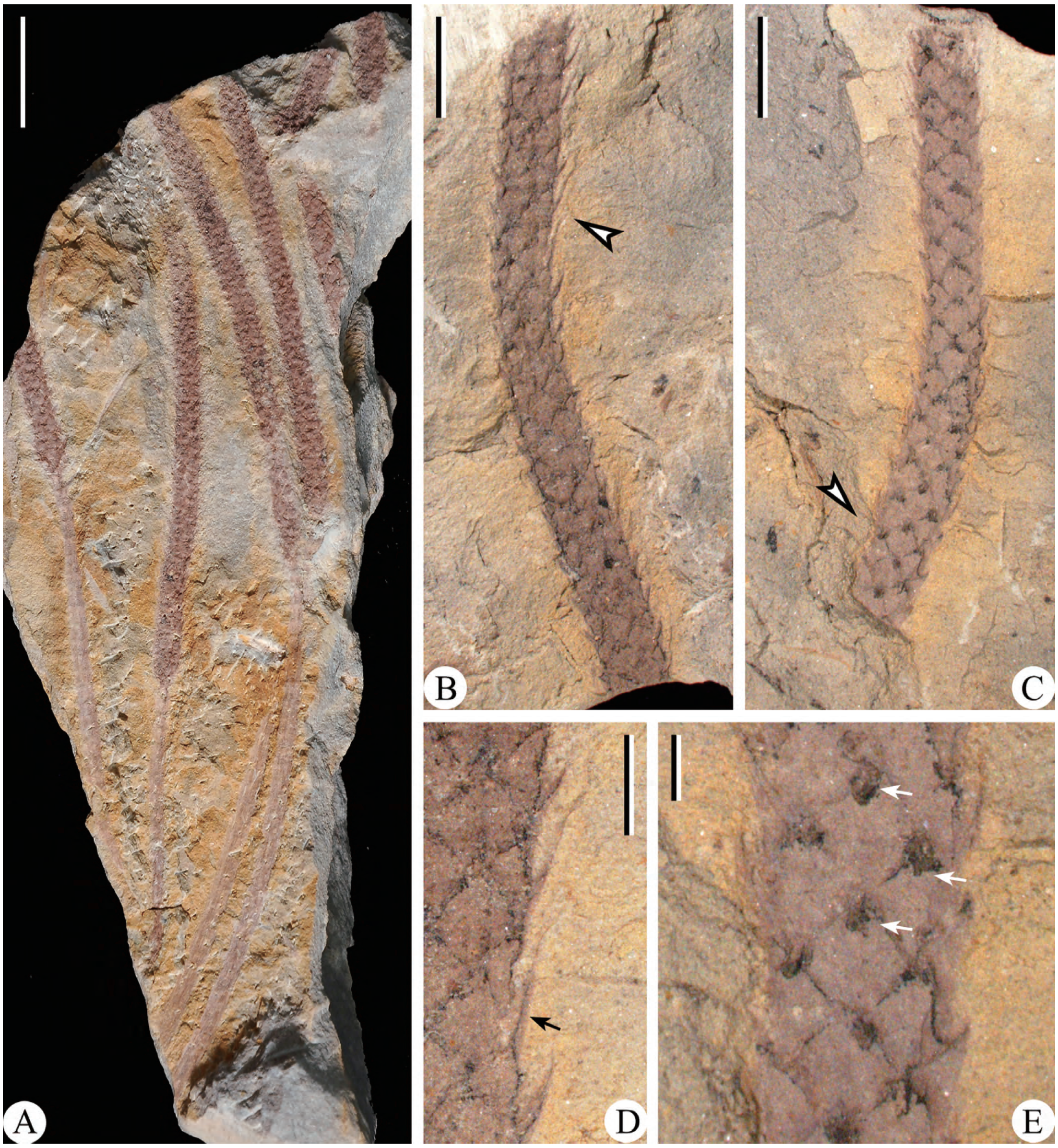
3　DESCRIPTION

Three different kinds of lycopsid strobili are distinguished in our collection and are temporarily referred to as Type A, Type B and Type C herein, respectively. One specimen of Type A shows four slender fertile axes arranged directionally on the bedding plane, with each bearing a terminal strobilus (Text-fig. 3-A). Fertile axes are unbranched, ca. 0.9 mm wide and up to 5.2 cm long. Strobili, 2.2—2.9 mm wide and up to 4.5 cm long, are incomplete in length, either broken at upper part

(Text-fig. 3-A) or at both ends (Text-fig. 3-B, 3-C). Both strobili and fertile axes have no discernable change in width along their length. Rhombic impressions and thin linear extensions of sporophylls separately occur on the surface and along the lateral sides of strobili (Text-fig. 3-B—E). We interpret the rhombic impressions and the linear extensions as the sporophyll laminae and distal tips of sporophylls, respectively; that is, each sporophyll possesses a rhombic lamina and a distal linear tip.

On the upper corner of these rhombic impressions, there is usually an area filled with dark coalified material, probably representing the scar of a broken sporophyll tip (Text-fig. 3-E, arrows). The sporophyll pedicels and sporangia are not observed, which might have decayed during preservation, or been highly compressed and then covered by the sporophyll laminae (see Section 4.1 for a taphonomic discussion).

Sporophylls are arranged in alternating pseud-



Text-figure 3 Type A strobili from the Upper Devonian (Frasnian) of Hunan Province, China.

A. Slender fertile axes bearing terminal strobilus. Strobili and axes are arranged directionally. PKUB17201. Scale bar = 1 cm. B, C. Part and counterpart of a strobilus, displaying sporophylls arranged in alternate pseudowhorls, parastichies and orthostichies. Portions indicated by arrows in B and C are enlarged in D and E, respectively. PKUB17202a, PKUB17202b. Scale bars = 5 mm. D. Enlargement of the strobilus in Figure 3-B (arrow), showing its lateral side. Arrow points to a linear sporophyll tip. Scale bar = 2 mm. E. Enlargement of the strobilus in Figure 3-C (arrow), showing front view of rhombic sporophyll laminae. Arrows indicate scars left by the removal of sporophyll tips. Scale bar = 1 mm.

owhorls, and show clear parastichies and orthostichies. The angle between the sporophyll parastichies and the supposed horizontal line is ca. 50°. In one single pseudowhorl, either three or two sporophylls are visible on the surface of strobili that is oriented to observer, and it is expected that there are one or two more sporophylls that extend into to the rock matrix, correspondingly. Thus, there are four sporophylls in each pseudowhorl.

Rhombic laminae of sporophylls are 1.8—2.1 mm high and 1.6—2.0 mm wide. Along the side of strobili, linear tips of laterally preserved sporophylls are connected to the upper corner of laminae (Text-fig. 3-D, arrow). The tips are ca. 3.2 mm long and ca. 0.2 mm wide at base, departing from strobili with angles of 13°—25°. In front view, the linear tips are generally not preserved. Areas with dark coalified material, or the probable scars of broken sporophyll tips are ca. 0.5 mm long and ca. 0.6 mm wide, occupying the upper one-fourth of rhombic laminae (Text-fig. 3-E, arrows).

The other two undetermined lycopsids, or the Type B and Type C, are also found from the bed containing Type A. Two strobili of Type B are complete in length, terminating fertile axes (Text-fig. 4-A, 4-B). The strobili are overall cylindrical and slightly curved, 9.0—9.5 cm long and ca. 8.0 mm wide at base, and decrease in width acropetally. Sporophylls are helically arranged, with angles between the parastichies (Text-fig. 4-C, dashes) and the supposed horizontal line of ca. 30°. The sporophylls are linear in both front view (Text-fig. 4-C, rectangle) and lateral view (Text-fig. 4-C, 4-D), 15—20 mm long and ca. 0.2 mm wide. The basal parts of sporophylls expand slightly, exhibiting a triangular shape in lateral view (Text-fig. 4-D, arrow 1). Sporophylls depart from the strobilar axis at angles of ca. 30° and then curve abaxially (Text-fig. 4-D, arrow 2), and tips of some sporophylls are nearly perpendicular to the strobilus. The strobilar axes are ca. 1.0 mm wide (Text-fig. 4-E). The subtending fertile axes are similar in width with strobilar axes (Text-fig. 4-A, 4-B), bearing a few vegetative microphylls that depart at angles of ca. 60° (Text-fig. 4-B, arrow 2; 4-F). One microphyll curves adaxially at its half-length (Text-fig. 4-F, arrow). The microphylls are linear with smooth margins, up to 7.6 mm long and ca. 0.2 mm wide.

Strobili of Type C are cylindrical, up to 6.8 cm long and 4.6—6.5 mm wide (excluding the distal part of sporophylls, Text-fig. 4-G—I). The widths do not change significantly along most of the lengths of strobili except for the distal tips, which are blunt in shape. One strobilus exhibits a bifurcation at an angle of ca. 60° (Text-fig. 4-G), forming two daughter strobili of similar widths. Sporophyll laminae are lanceolate in shape (Text-fig. 4-G, arrow), 0.6—1.1 cm long and ca. 1.8 mm in maximum width. Most of the sporophyll laminae are abaxially curved (Text-fig. 4-H, arrow; 4-I, arrow).

4 COMPARISONS AND DISCUSSION

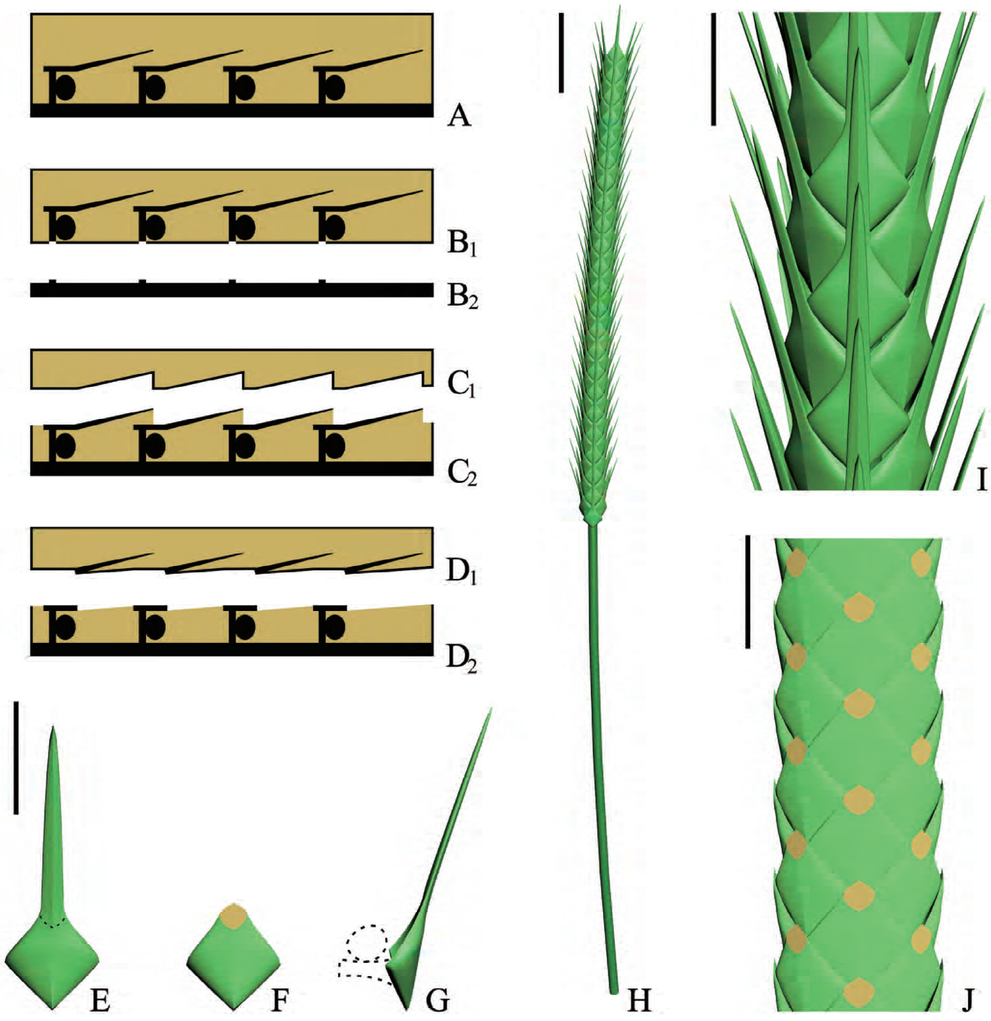
4.1 Taphonomy of strobili

For lycopsid axes preserved as impression and compression, the rock fractures along different planes will result in various appearances (e.g., Rex and Chaloner, 1983; Edwards and Benedetto, 1985). We consider that compression fossils of strobili may perform similarly (Text-fig. 5-A—D). The strobilus in rock matrix (Text-fig. 5-A) has three potential fracture planes: 1) through proximal parts or bases of sporophyll pedicels (Text-fig. 5-B_1, 5-B_2); 2) along the surface of sporophylls (Text-fig. 5-C_1, 5-C_2) and (3) through the middle parts of sporophylls to separate laminae and tips (Text-fig. 5-D_1, 5-D_2). In the first case, strobilar axes may be exhibited, and in the second case, only sporophylls would be visible. These two cases are evident in our collection; for example, a strobilus of Type B displays front views of sporophylls in the upper part (Text-fig. 4-C, rectangle) and strobilar axis in the lower part (Text-fig. 4-E), indicating a fracture plane running

Text-figure 4 Two undetermined lycopsid strobili (A—F. Type B; G—I. Type C) from the Upper Devonian (Frasnian) of Hunan Province, China.

A. A complete strobilus terminating a fertile axis. PKUB17203. Scale bar =1 cm. B. Another complete strobilus terminating a fertile axis. PKUB17204. Scale bar =1 cm. C. Enlargement of the strobilus in Text-fig. 4-A (arrow 1), showing helically arranged sporophylls in front view (rectangle), and linear sporophylls in side view. Dashes indicates the parastichies formed by sporophylls. Scale bar =5 mm. D. Enlargement of the strobilus in Text-fig. 4-B (arrow 1), showing sporophylls. Arrow 1 indicates the basal expansion of a sporophyll, and arrow 2 indicates an abaxially-curved sporophyll. Scale bar =5 mm. E. Enlargement of the strobilus in Text-fig. 4-A (arrow 2), showing strobilar axis in the middle. Scale bar =2 mm. F. Enlargement of the strobilus in Text-fig. 4-B (arrow 2), showing subtending axis. The axis bears several vegetative microphylls. One microphyll recurves adaxially at its half-length (arrow). Scale bar =2 mm. G. Bifurcate strobilus displaying lanceolate laminae of sporophylls (arrow). PKUB17205. Scale bar =1 cm. H, I. Strobili displaying sporophylls with abaxially curved laminae (arrows). PKUB17206, PKUB17207. Scale bar =1 cm.

through different levels. Besides present Type B, there are numerous other examples for these two cases among compression fossils of Late Devonian lycopsid strobili (e. g., Meng *et al.*, 2013, 2016; Wang *et al.*, 2014, 2017). Considering that the strobili of Type A demonstrate linear tips along the lateral sides and scars on the impressions of sporophyll laminae in front view (Text-fig. 3-B, 3-C), the fracture plane of these specimens probably represents the third case, in which the sporophyll laminae and tips were separated (Text-fig. 5-D_1, 5-D_2). In this case, the tip scars resembles the "false leaf scar" on the leaf bases of some Devonian and Lower Carboniferous lycopsids, including *Sublepidodendron*, *Tomiodendron* and *Eskdalia* (Mensah and Chaloner, 1971; Thomas and Purdy, 1982; Wang *et al.*, 2003a). The preservation status of Type C is uncertain because of limited material.



Text-figure 5　Taphonomic explanation for compression fossils of strobili (A—D) and partial reconstruction of Type A strobili and sporophylls (E—J). Scale bars: 2 mm for E—G, I, J; 5 mm for H.

A—D. Interpretative line drawings of preservation of a compressed strobilus in rock matrix (A) and broken patterns along different rock fracture planes (B—D), which is expected to result in different surface appearances in the compression fossils of the strobilus. Brown and black colors indicate rock matrix and strobilus remains, respectively. Each sporophyll illustrated herein consists of a pedicel bearing a sporangium, a lamina and a tip. B_1, B_2. Fracture plane through the proximal parts of sporophyll pedicels, and compression fossils exhibiting strobilar axes; C_1, C_2. Fracture plane along the surface of sporophylls; D_1, D_2. Fracture plane separating sporophyll laminae and their tips. E—G. Reconstruction of a sporophyll. E. Front view; F. Front view with the removal of sporophyll tip, exhibiting a tip scar (colored in yellow); G. Lateral view. Black dashes in E indicate the probable fracture position of the sporophyll tip. Black dashes in G indicate supposed location of pedicel and sporangium. H. Reconstruction of a fertile axis bearing a terminal strobilus. I. Enlargement of strobilus in H, displaying sporophylls arranged in parastichies, orthostichies and alternate pseudowhorls. J. Reconstruction of a strobilus showing an appearance similar to the specimen shown in Text-fig. 3-E, interpreted as being formed by two sequential processes: 1) compression and decay of sporangial material during perservation; and 2) removal of all sporophyll tips during rock fracture (with a pattern as in Text-fig. 5-D_1, 5-D_2).

Based on the descriptions, and with taphonomic factors taken into consideration, sporophylls and strobili of Type A are reconstructed as in Text-fig. 5-E—I. The preservation and rock fracturing processes for such a strobilus can be simulated in a three-dimensional model in Text-fig. 5-J, and its surface displays an appearance closely comparable to that in Text-fig. 3-E, when the strobilus was compressed and then the sporophyll tips were removed. This simulation supports our deduction that the scars on sporophyll laminae are left by the splitting of sporophyll tips.

4.2 Comparison between Type A strobili and related taxa

The slender strobili of Type A exhibit tiny sporophylls arranged in alternate pseudowhorls of four, differing from other lycopsids of the Middle and Late Devonian age including *Longostachys latisporophyllus* in Cai and Chen (1996); *Yuguangia ordinata* in Hao *et al*. (2007); *Minostrobus chaohuensis* in Wang (2001) and Meng *et al*. (2013, 2015); *Lepidostrobus xingjiangensis* in Wang *et al*. (2003b); *Sublepidodendron songizense* in Wang *et al*. (2003a) and Meng *et al*. (2014); *S. grabaui* in Wang and Xu (2005) and Meng *et al*. (2016); *Changxingia longifolia* in Wang *et al*. (2014); *Changxingia* sp. in Wang *et al*. (2017); *Cymastrobus irvingii* in Evreïnoff *et al*. (2017) and *Kowieria alveoformis* in Gess and Prestianni (2018). *Oxroadia conferta* and *Paurodendron fraiponti* are two Carboniferous pseudoherbaceous lycopsids possessing bisporangiate strobili, which consist of sporophylls arranged in alternate pseudowhorls of four (Schlanker and Leisman, 1969; Bateman, 1992). Such phyllotaxy resembles that of Type A. However, the strobili of the two Carboniferous plants are shorter and wider, and do not possess significant tips on sporophylls. The surface appearance of Type A strobili recalls stems of *Leptophloeum rhombicum*, a worldwide distributed arborescent lycopsid in the Late Devonian (Li *et al*., 1986; Wang *et al*., 2005; Prestianni and Gess, 2014). However, it is the sporophyll laminae rather than vegetative leaf cushions that display rhombic shape in Type A strobilus. *L. rhombicum* usually has an oval leaf scar in the middle of each leaf cushion, while the sporophyll tip scar of Type A is located at the upper corner of rhombic lamina. Besides, the leaf cushions of *L. rhombicum* are much larger than the sporophyll laminae of Type A and do not arrange in pseudowhorls of four. Considering the comparisons given above, the Type A strobili display not only unique characteristics such as slender strobili and rhombic sporophyll laminae arranged in alternate pseudowhorls of four, but also sufficient differences with the known Devonian lycopsid taxa. However, the establishment of a new taxon is restrained by the lack of specimens.

4.3 Type B and Type C

Most Devonian members of the Order Isoëtales *sensu lato* possess sporophylls that are evidently differentiated into a horizontal pedicel and an upturned lamina, such as *Yuguangia ordinata* in Hao *et al*. (2007), *Minostrobus chaohuensis* in Meng *et al*. (2013) and *Changxingia longifolia* in Wang *et al*. (2014). However, the sporophylls of Type B (Text-fig. 4-A—F) seem to lack a distinct pedicel and are obliquely attached to the strobilar axes. Comparable sporophylls of the Givetian *Longostachys latisporophyllus* (Cai and Chen, 1996) have no pedicel but bear hair-like ornamentation along margins, differing from the entire margin in our specimens.

Distinct bifurcated strobili, as in Type C, are also described in the Givetian *Yuguangia ordinata* from Yunnan, South China, and Famennian *Hefengstrobus bifucus* from Xinjiang, Northwest China (Xu and Wang, 2002; Hao *et al*., 2007), and both of them possess sporophylls with dentate margins and upturned laminae. With similar dimensions and bifurcating nature, the strobili of Type C (Text-fig. 4-G—I) recall *Y. ordinata* and *H. bifucus*, but differ from the latter two in sporophylls displaying entire margins and abaxially curved laminae. Considering the deficiency of detailed knowledge on the two lycopsid strobili in our collection, we decide not to assign them into any already known taxa at present.

4.4 Evolutionary implications

The three lycopsids described in this paper are of Frasnian age, an interval with a relatively low diversity compared to the prosperity in the Famennian (Cascales-Miñana, 2016). Several Frasnian lycopsids demonstrating vegetative axes were reported from different localities around the world, including cf. *Longostachys* sp. and tree-shaped *Chamaedendron multisporangiatum* from South China (Schweitzer and Li, 1996; Xue and Hao, 2007), the protolepidodendraleans *Colpodexylon deatsii*, *Colpodexylon cachiriense* and *Haskinsia sagittata* from North and South America (Banks, 1944; Edwards and Benedetto, 1985), arborescent *Protolepidodendropsis pulchra* from Svalbard (Berry and Marshall, 2015) and cosmopolitan *Leptophloeum rhombicum* (Li *et al.*, 1986; Wang *et al.*, 2005). However, the deficient strobilus fossils in the Frasnian hampered the further understanding on lycopsid reproductive organs. Established on the basis of permineralized material from Northwest China, *Lepidostrobus xingjiangensis* is one of the best strobili known from the Frasnian or Frasnian-Famennian boundary (Wang *et al.*, 2003b). cf. *Longostachys* sp. demonstrates partially preserved strobili and isolated spoon-shaped sporophylls (Xue and Hao, 2007). *Sphinxiocarpon wuhanium* (Li *et al.*) Wang *et al.* from South China is a Frasnian seed-like propagule regarded as with a possible lycopsid affinity (Xue, 2010; Xu *et al.*, 2012), while its strobili remain unclear. The "multisporangiate sporophylls" (i.e., a single sporophyll bearing multiple sporangia) in *Chamaedendron multisporangiatum* (Schweitzer and Li, 1996) appear problematic in configuration, since all other lycopsids bear only one sporangium on a sporophyll. Our findings, with three divergent types of strobili, add to the diversity of Frasnian lycopsid reproductive organs.

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