

Lochkovian plants from the Xitun Formation of Yunnan, China, and their palaeophytogeographical significance

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Abstract – A megafossil plant assemblage containing three zosterophyll plants (Gen. nov. A, aff. *Huia* sp. and a unnamed spike) is described from the Lower Devonian Xitun Formation (Lochkovian) of Qujing, Yunnan Province, China, providing new data on the diversity of plant types during the Lochkovian, a time poorly represented by fossil vascular plants. Gen. nov. A has a character combination of naked axes, a diagnostic branching pattern (i.e. K-type branching as well as small lateral branches scattered along the axes) and lateral stalked sporangia. Aff. *Huia* sp. has ovate and stalked sporangia which are arranged in loose spirals and are reflexed adaxially. Combining the plants previously reported from the Xitun Formation (i.e. *Xitunia spinitheca*, *Zosterophyllum shengfengense* and *Z. minorstachyum*), the Xitun flora is dominated by zosterophylls and exhibits varied vegetative and fertile morphologies. Unlike the coeval plant assemblages in many localities of Laurussia and western Gondwana, which are mainly composed of plants with isotomous branching and terminal sporangia, the Lochkovian flora of South China is dominated by zosterophylls, documenting the existence of a distinct Northwest Gondwanan phytogeographic unit in the Lochkovian and a strong effect of phytogeographical isolation.

Keywords: Lochkovian, phytogeography, zosterophyll, plant diversity, South China.

1. Introduction

Plants from the Silurian to Early Devonian period are crucial to our understanding of the primary diversification of tracheophytes and their phytogeographical distribution patterns (Edwards & Wellman, 2001). The earliest uncontroversial records of embryophytes are the Dapingian (early Middle Ordovician) cryptospores from the Zanjón Formation and the Labrado Formation of Argentina (Rubinstein *et al.* 2010). Some workers have suggested that the enigmatic plant *Pinnatiramosus qianensis* Geng, from Llandovery sediments (lowermost Lower Silurian) of Fenggang, Guizhou Province, China is the earliest known vascular plant (Geng, 1986; Cai *et al.* 1996; Wang & Xu, 2009), while others claimed that this plant may be rooting structures of younger (i.e. Permian) vegetation (Edwards *et al.* 2007). Wenlock sediments (late Early Silurian) are presently the lowermost horizons with uncontroversial fertile axial land plants (Edwards, Feehan & Smith, 1983). Nevertheless, the Silurian *Baragwanathia* flora in Victoria, Australia is of Ludlow age based on graptolite records (Tims & Chambers, 1984; Rickards, 2000), which indicates an early appearance of lycophytes. Recently, some morphologically complex plants of mainly zosterophyll affinities were described from the Ludlow sediments of Bathurst Island, Canada (Basinger, Kotyk & Gensel, 1996; Kotyk *et al.* 2002).

The remains of megafossil plants are progressively more common in Pridoli (uppermost Silurian) and Lochkovian (lowermost Lower Devonian) strata, as reported from England, Wales, Brazil, Xinjiang (North China), Yunnan (South China), Argentina and other areas (Cai, Dou & Edwards, 1993; Wellman *et al.* 2000; Edwards & Wellman, 2001 and references therein; Edwards *et al.* 2001a,b; Gerrienne *et al.* 2001, 2006; Hao *et al.* 2007, 2010; Xue, 2009; Wang & Xu, 2009).

In previous reports, four species of *Zosterophyllum* Penhallow (*Z. qujingense* Hao *et al.*, *Z. xishanense* Hao *et al.*, *Z. minorstachyum* Xue and *Z. shengfengense* Hao *et al.*) and one plant with distinct sporangial features, *Xitunia spinitheca* Xue, have been described from Pridoli–Lochkovian sediments in Qujing, Yunnan, South China (Hao *et al.* 2007, 2010; Xue, 2009). The present paper adds new data on the primary diversity of plants in this area and presents a new zosterophyll-dominated plant assemblage from the Xitun Formation (Lochkovian) of Qujing.

2. Stratigraphy

The Lower Devonian deposits in the Qujing area of Yunnan Province, China, include, in ascending order, the Xiaxishancun Formation, Xitun Formation, Guijiatun Formation and Xujiachong Formation, and overlie the Silurian Yulongsi Formation (Fig. 1, also see figs 1 & 2 in Dupret & Zhu, 2008) (Li & Cai, 1978; Cai *et al.* 1994; Fang *et al.* 1994; Ma, Liao &

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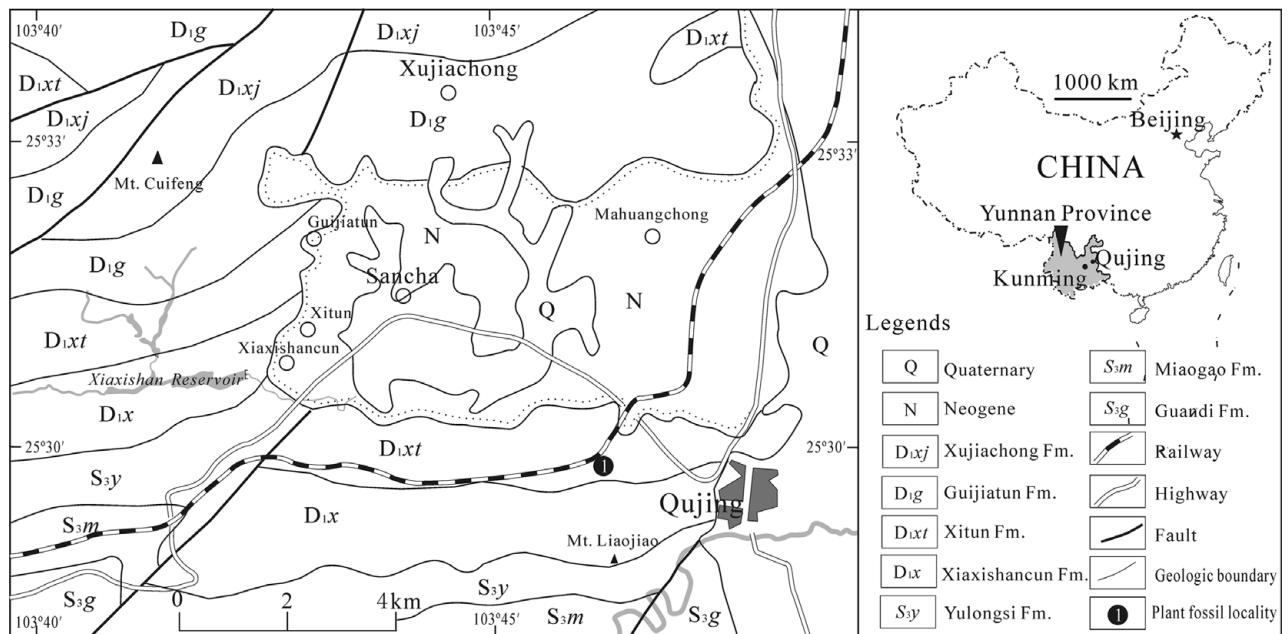


Figure 1. Generalized map showing geologic features of the Qujing area and plant fossil locality (modified from fig. 1 of Hao *et al.* 2007).

Wang, 2009). The Xitun Formation is well exposed near Qujing city (Fig. 1). Previous reports of plants from this formation include only plant fragments preserved as isolated sporangia and K-type sterile branches (possibly of *Zosterophyllum*), and fragments of algae such as *Uncatoella verticillata* Li & Cai (Li & Cai, 1978; Kenrick & Li, 1998; Cai & Wang, 1995). Two more plants, *Xitunia spinitheca* and *Z. minorstachyum*, were added to this list recently (Xue, 2009).

The Xitun Formation consists mainly of greyish blue and purple calciferous mudstones, which yield abundant bivalves, fish and rare fragmentary megafossil plants. Fish remains have been assigned to the *Diabolepis–Nanpanaspis* macrovertebrate assemblage II *sensu* Zhu, Wang & Wang (2000) and the Cuifengshan assemblage *sensu* Zhao & Zhu (2010), indicating a mid–late Lochkovian age. On the basis of spore assemblages, a mid–late Lochkovian age (Early Devonian) was proposed for the Xitun Formation by Cai *et al.* (1994). The spores they obtained from this formation include *Apiculiretusispora plicata*, *Stenozonotriletes pusillus*, *Breconisporites breconensis*, *Streelispora newportensis*, *Apiculatisporites microcanonus* and *Emphanisporites neglectus*, comparable to assemblages of the *Streelispora newportensis–Emphanisporites microratus* (NM) and *Breconisporites breconensis–Emphanisporites zavallatus* (BZ) zones of the Old Red Sandstone of Europe (Richardson & McGregor, 1986; Streele *et al.* 1987; Cai *et al.* 1994). However, Tian & Zhu (2009) suggested that the Siluro-Devonian boundary should be located at the middle of the Xitun Formation, based on their recovery of spore assemblages of the *Synorisporites verrucatus–Apiculiretusispora plicata* (VP) and *Apiculiretusispora minuta–Leiotriletes ornatus* (MO) types. While the Early Devonian megafossil plants of South China show many endemic forms (see discussion), the reported

spore assemblages of the Xitun Formation share many elements with those of Europe (Laurussia). Further investigation of dispersed spores and *in situ* spores of endemic plants is badly needed considering the controversy over spore biostratigraphy of this formation and the apparent contradiction between evidence from megafossils and spores.

Some beds of the Xitun Formation are dominated by the bivalve *Dysodonta* Mansuy, an Early Devonian genus found in Northern Vietnam and the Yunnan and Guangxi provinces of China, and the associated brachiopod genus *Lingula* (Fang *et al.* 1994). Ostracods collected from the mid–upper part of the Xitun Formation include *Cytherellina suboviformis* Wang *et al.*, *Sulcella convaviscula* Wang *et al.*, *Paracoeloneilla fabiformis* Wang *et al.* and *Leperditia delicata* Jiang, indicating an age of early Early Devonian (but not younger than Pragian) (Wang, Liu & Li, 1992). Conodont records give little additional insight into the age of the Xitun Formation; some taxa of Ludlow–Pridoli age, *Ozarkodina crispera*, *O. excavate* and *Dentacodina* sp., were found in the upper part of the underlying Yulongsi Formation (Fang *et al.* 1994), but conodonts were not recovered from the mainly clastic Xiaxisancun and Xitun formations.

A mid–late Lochkovian age for the Xitun Formation has been questioned by some authors. Based on faunal records (fish, chitinozoans and others) of the Yulongsi Formation, Rong *et al.* (1990) suspected that at least the lower part of the Xiaxisancun Formation might be of Pridoli age, which indicates that the overlying Xitun Formation could be slightly older than mid–late Lochkovian, perhaps early–mid Lochkovian. Wang (1997) established a vertebrate assemblage, *Parathelodus–Polybranchiaspis* assemblage, in the Xiaxisancun and Xitun formations and suggested on this basis that both of these formations are of Pridoli age.

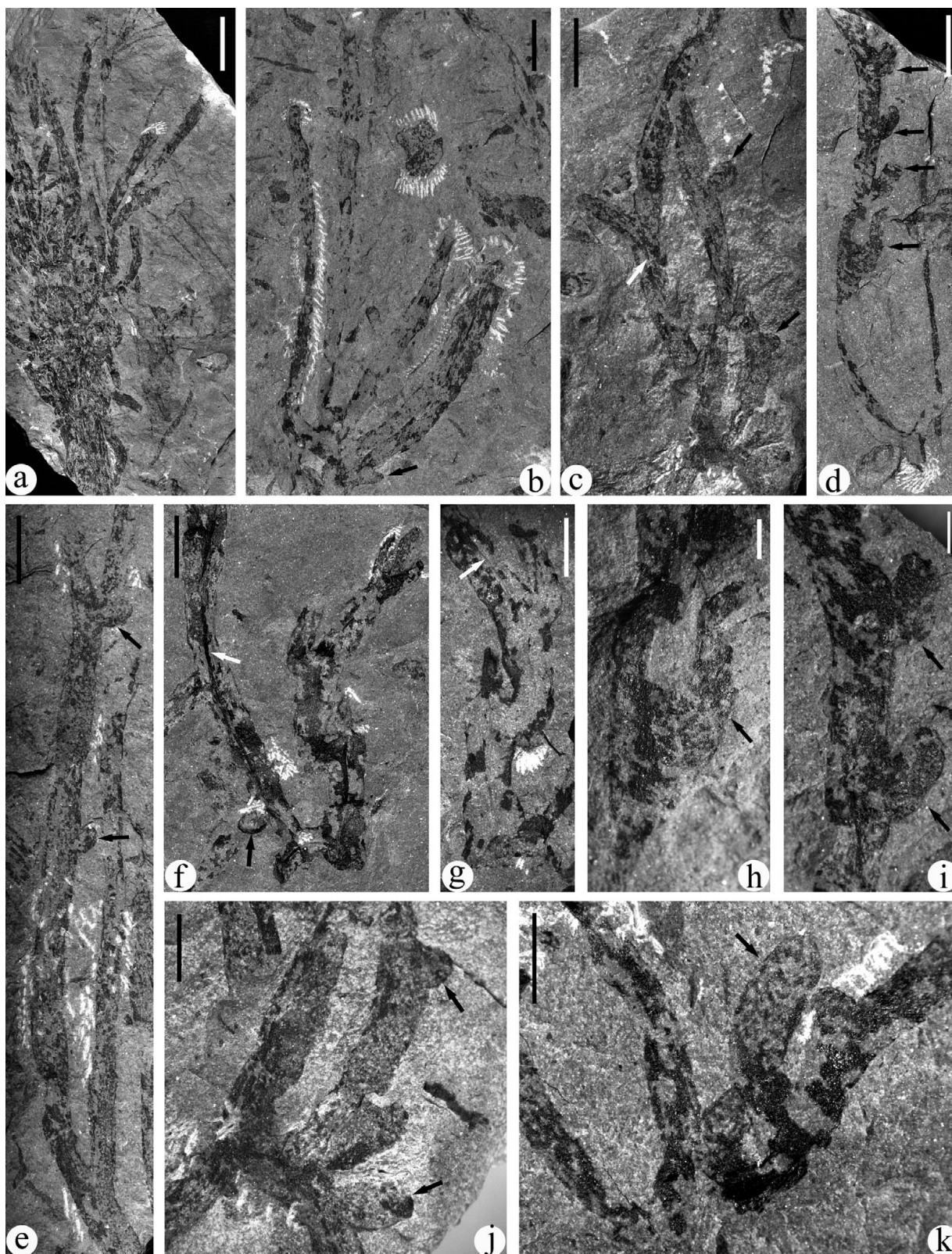


Figure 2. Gen. nov. A from the Xitun Formation of Yunnan, China. (a) Multiple overlapping axes, probably reflecting the crowded state of a living plant, whereby a rhizome bears numerous upright branches. PKU-XH204a. Scale bar = 10 mm. (b) Five upright axes arising from a central rhizome. Black arrow (bottom) indicates a small lateral branch. PKU-XH203. Scale bar = 5 mm. (c) Axes. Black arrows indicate two small lateral branches. White arrow indicates xylem strand vestige. The lower part is enlarged in (j). PKU-XH202a. Scale bar = 4 mm. (d) Axis showing a proximal dichotomy and four small lateral branches distally. PKU-XH206. Scale bar = 4 mm. (e) Upright axes with small lateral branches (arrows). PKU-XH205. Scale bar = 4 mm. (f) Axis showing K-type branching, small lateral branch (black arrow) and vestige of central xylem strand (white arrow). PKU-XH218. Scale bar = 5 mm. (g) Axis showing branching and vestige of central xylem strand (white arrow). PKU-XH220. Scale bar = 3 mm. (h) Enlargement of the lower small lateral branch in (d). Scale bar = 1 mm. (i) Enlargement of the upper part of (d). Scale bar = 1 mm. (j) Enlargement of the lower part of (c), showing K-type branching. Arrows refer to two small lateral branches. Scale bar = 2 mm. (k) Axis with a small lateral branch (arrow). PKU-XH202a. Scale bar = 2 mm.

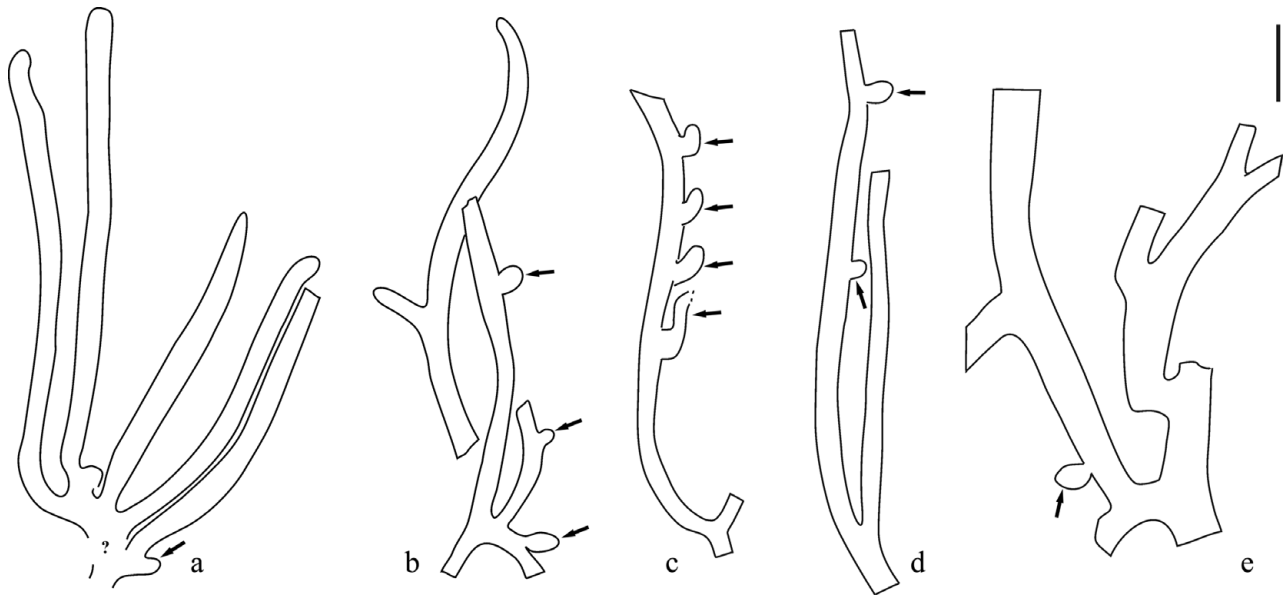


Figure 3. Line drawings of the axes of Gen. nov. A. (a–e) Axes shown in (a) Figure 2b, (b) Figure 2c, (c) Figure 2d, (d) Figure 2e and (e) Figure 2f. Scale bar = 5 mm.

3. Materials and methods

The plant fossils studied here were collected from the middle–upper part of the Xitun Formation, cropping out in a quarry in Huaguo Hill, Shengfeng district of Qujing city, Yunnan, China (Fig. 1); the GPS location is at 25° 29.853' N and 103° 46.309' E (WGS84). The fossils described in this report were derived from a c. 10 cm thick bed of grey mudstone, which also contains fossils of the previously described *Xitunia spinitheca*. *Zosterophyllum shengfengense* was collected from a bed of grey mudstone overlying this unit (Hao *et al.* 2010). Specimens have been prepared by disaggregation with steel needles, and photographed with a Nikon digital camera system (Nikon SMZ1500, DXM1200F and Software NIS-Elements). All specimens are housed at the School of Earth and Space Sciences, Peking University, P. R. China.

4. Palaeobotanical descriptions

4.a. Gen. nov. A (Figs 2a–k, 3a–e, 4a–f, 5a–b)

4.a.1. Description

More than 15 specimens with sterile axes have been collected. Axes are naked and range from 1.2 to 3.1 mm in width (Fig. 2 a–g). The longest axis preserved is 41 mm long and incomplete at both ends. A vestige of a central xylem strand occurs along the axes (Fig. 2c, f, g, white arrows). In some examples the axes are compressed together (Fig. 2a), which may be a reflection of the living status, with many crowded upright axes arising from a common rhizome. Figure 2b shows a rhizomatous axis with more than five upright axes; these upright axes may arise from successive K- or H-type branching patterns at very close intervals (Figs 2b, 3a). The axis shown in Figure 2c divides twice at the base to form a K-type branching configuration

(Figs 2c, j, 3b). Some axes are wider in diameter and branch at close intervals, with a clear vestige of a xylem strand (Figs 2f, g, 3e). The upright axes may branch dichotomously (Figs 2c–e, 3b–d) or not (Figs 2b, 3a).

Small lateral branches with round or tapering apices are irregularly distributed along the axes (Figs 2b–f, 3a–e, black arrows). They are of various dimensions, 1.0–1.5 mm in width and 0.8–4.3 mm in length. Their distribution and morphology are different from those of the normal dichotomous and K-type branching patterns. Some are borne on the axes at a position close to the branching point of K-type branching (Figs 2b, f, j, k, 3a, b, e). Others are attached to one of the daughter branches of a dichotomous axis (Figs 2d, e, 3c, d), with an interval ranging from 3.8 to 13.4 mm. Some of these kinds of branches are very small and appear as elliptical ‘protuberances’ on the axes (Fig. 2d, i), while others are much larger (Fig. 2d, h, k). The specimen shown in Figure 2d shows the size variation of these branches. The axis shown in Figure 2d firstly divides once at the proximal portion to form a dichotomy and one of the daughter axes bears four small lateral branches (Figs 2d, 3c, black arrows), the first one of which, although broken at the tip, is larger than the others (Fig. 2h, i).

Although not organically connected to the sterile axes, four fertile axes (Fig. 4a, b, d, e) are considered parts of this plant because of their general morphology, axis size, surface pattern and similar appearance of vestiges of a central xylem strand. Specimens PKU-XH216 and 217b contain two incompletely preserved axes, each bearing three lateral sporangia (Fig. 4a, b, arrows; Fig. 5a, b). The axes are naked, ranging from 1.1 to 1.6 mm in width, and up to 33 mm in length. Sporangia are stalked and have a loose and irregular arrangement (Figs 4c, 5a, b), with an irregular distance between successive sporangia, from 3.1 mm proximally to 9.4 mm distally in specimen PKU-XH216 (Fig. 4a). The third fertile axis is 1.2–1.4 mm

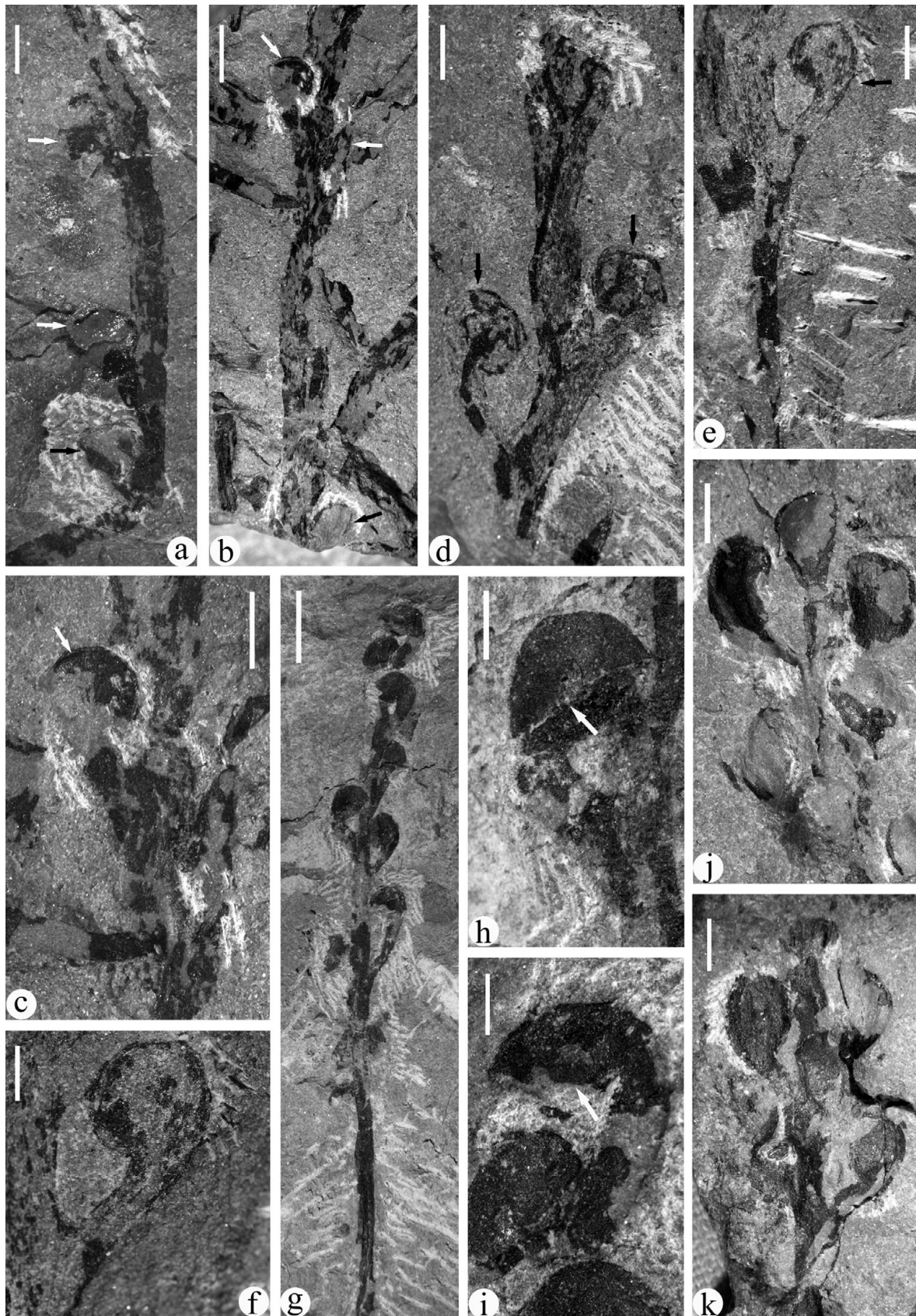


Figure 4. Gen. nov. A (a–f), aff. *Huia* sp. (g–i) and an unnamed spike (j, k) from the Xitun Formation of Yunnan, China. (a, b) Two fertile axes with lateral sporangia attached (arrows). (a) PKU-XH216. Scale bar = 2 mm. (b) PKU-XH217b. Scale bar = 3 mm. (c) Enlarged view of the upper two sporangia of the axis in (b). Arrow indicates a narrow thickened border. Scale bar = 2 mm. (d) Fertile axis with two lateral stalked sporangia (arrows). PKU-XH213. Scale bar = 3 mm. (e) Fertile axis with a lateral sporangium (arrow). PKU-XH209. Scale bar = 2 mm. (f) Enlarged view of the sporangium in (e). Scale bar = 1 mm. (g) Spike with helically arranged sporangia. PKU-XH214. Scale bar = 4 mm. (h, i) Enlarged view of sporangia, showing their recurvature and dehiscence (arrows). Scale bars = 1 mm. (j, k) Unnamed spike, part and counterpart, showing helically arranged sporangia. PKU-XH215a, 215b. Scale bars = 2 mm.



Figure 5. Line drawings of Gen. nov. A, aff. *Huia* sp. and the unnamed spike. (a) Fertile axis shown in Figure 4a. Scale bar = 2 mm. (b) Fertile axis shown in Figure 4b. Scale bar = 3 mm. (c) aff. *Huia* sp., spike shown in Figure 4g. Scale bar = 2 mm. (d, e) Unnamed spike shown in Figures 4j, 4k. Scale bar = 1.5 mm.

in width and 13.4 mm in length, broken at the proximal end (Fig. 4d); it bears two lateral stalked sporangia. Two dichotomies can be observed at the very distal part of this axis. The fourth axis similarly bears one lateral sporangium (Fig. 4e, f). The sporangia are circular to elliptical in shape, 1.8–2.4 mm wide and 1.8–2.3 mm high. Each sporangium is stalked, departing from the axis at a narrow angle. The stalk is 2.4–2.8 mm long and 0.7–1.2 mm wide, and the distal part of the stalk is wider than the basal part, merging with the margin of the sporangia. A very narrow thickened border is visible on the sporangia (Fig. 4c, arrow), indicating the position of dehiscence.

4.a.2. Comparisons and affinity

Although fragmentarily preserved, Gen. nov. A shows a unique character combination that includes K-type branching, lateral stalked sporangia and diagnostic small lateral branches scattered along the axes. The first two characters suggest that Gen. nov. A is clearly a zosterophyll plant. The K-type branching, resulting from two successive dichotomies at closely spaced intervals, resembles that of most zosterophylls, such as *Zosterophyllum*, *Kaulangiophyton* Gensel *et al.*, *Discalis* Hao and *Gumuia* Hao (Walton, 1964; Gensel, Kasper & Andrews, 1969; Edwards, 1975; Gensel, 1982a; Gerrienne, 1988; Hao, 1989a,b; Hao *et al.* 2007). The sporangia of Gen. nov. A, with a distal dehiscence, are more or less elliptical in shape and loosely arranged, similar to the sporangia of *Wenshania zhichangensis* Zhu & Kenrick, *Zosterophyllum deciduum* Gerrienne and *Z. shengfengense*, and to some specimens of *Z.*

myretonianum Penhallow where some sporangia are also more loosely arranged in fertile regions (Edwards, 1975; Gerrienne, 1988; Zhu & Kenrick, 1999; Hao *et al.* 2010). Nevertheless, unlike the sporangia of Gen. nov. A, the sporangia of *Z. myretonianum* and *Z. deciduum* have a clear junction between sporangium and stalk (Edwards, 1975; Gerrienne, 1988). Many other species of the genus *Zosterophyllum*, however, including *Z. myretonianum*, *Z. rhenanum* Krausel & Weyland, *Z. australianum* Lang & Cookson, *Z. yunnanicum* Hsü, *Z. qujingense*, *Z. sinense* Li & Cai, *Z. minorstachyum* and others (Walton, 1964; Edwards, 1975; Li & Cai, 1977; Hao, 1992; Hao *et al.* 2007; Wang, 2007; Xue, 2009), bear radial spikes with a compact arrangement of sporangia, and therefore differ from the specimens of Gen. nov. A.

The small lateral branches of Gen. nov. A, occurring at different levels of the plant, vary in size from small 'protuberances' to larger ones. These branches are obviously different from the normal K-type or dichotomous branching patterns of the same plant. Some short, non-circinate branches can be observed in the axes of *Zosterophyllum myretonianum*, *Z. deciduum* and *Z. xishanense* and they generally show as small protuberances (Lele & Walton, 1961; Gerrienne, 1988; Hao *et al.* 2007), similar to the smaller lateral branches of Gen. nov. A. The subordinate branches (also called axillary tubercles) of many zosterophylls (e.g. *Gosslingia* Heard, *Deheubarthia* Edwards *et al.*) are commonly positioned below the dichotomy of the main axial system (Kenrick & Crane, 1997, p. 152), different in position and distribution to the small lateral branches of Gen. nov. A. However, in *Tarella*

Edwards & Kenrick, subordinate branches of variable length and morphology are scattered over the main axes (Edwards & Kenrick, 1986), showing similarities to the condition of Gen. nov. A. In compression fossils, the subordinate branches are indicated by a conical projection or depression on the axes (Rayner, 1983; Remy, Schultka & Hass, 1986). In *Gosslingia*, *Deheubarthia*, *Tarella*, *Crenaticaulis* Banks & Davis, *Thrinakophyton* Kenrick & Edwards, *Anisophyton* Remy *et al.* and *Sawdonia* Hueber, the subordinate branches usually show as single, usually small, undeveloped, circinate axes (Remy, Schultka & Hass, 1986; Kenrick & Crane, 1997, p. 152), but the small lateral branches of Gen. nov. A do not show any circinate tips.

Apparently similar to the small lateral branches of Gen. nov. A, in the Rhynie Chert plant *Rhynia gwynne-vaughanii* Kidston & Lang, Edwards (1980) was able to describe the hemispherical projections and numerous short adventitious branches along the stem of *R. gwynne-vaughanii*, interpreting the latter as underdeveloped lateral branches or asexual reproduction structures. However, the similarity between small branches of Gen. nov. A and adventitious branches of *R. gwynne-vaughanii* must be considered as superficial in the absence of anatomical information for Gen. nov. A.

Based on the above comparisons, the present specimens probably represent a zosterophyll plant, with naked axes, a diagnostic branching pattern (i.e. K-type branching as well as small lateral branches scattered along the axes) and lateral stalked sporangia. Here they are treated as Gen. nov. A because the fragmentary preservation recommends against formal nomenclatural treatment at this time, and conditionally are assigned to the Zosterophyllopsida. Further assessment of the taxonomy and phylogenetic position of this plant requires more and better material.

4.b. aff. *Huia* sp. (Figs 4g–i, 5c)

Specimen PKU-XH214 bears a terminal spike (Figs 4g, 5c) 2.2–3.8 mm wide and about 23 mm in length, with the axis of the spike 0.8–1.1 mm wide. At least eight lateral sporangia are observed, which have a loosely helical arrangement (Fig. 5c). The sporangia are ovate in side view (Fig. 4h, i), 1.5–1.9 mm wide and 1.6–2.4 mm high. The distance between two successive sporangia is 1.2–5.4 mm. The sporangia have long stalks and are reflexed adaxially. A dehiscence line is visible on some sporangia, arching from one side of the sporangium over the adaxial face to the opposite side, dividing the sporangium into two unequal valves (Fig. 4h, arrow; Fig. 5c, dotted line). Some sporangia have been broken along the dehiscence line, leaving only one half attached on the stalk (Fig. 4i, arrow; Fig. 5c). The stalk is 0.6–1.0 mm wide and 2.0–3.9 mm long, broadening distally and merging with the margin of the sporangia, lacking a clear junction between stalk and sporangium.

The distinguishing feature of the plant is the ovate and stalked sporangia arranged in loose helices and

reflexed adaxially (as in specimen PKU-XH214). These sporangia resemble those of *Huia recurvata* Geng and *H. gracilis* Wang & Hao described from the Pragian deposits of Yunnan, China (Geng, 1985; Wang & Hao, 2001). *Huia* bears terminal spikes comprised of helically arranged lateral sporangia and a probable centrarch protostele; it remains controversial in affinity, being considered variously a rhyniophyte (Geng, 1985; Gensel, 1992), a *Cooksonia* derivative (Wang & Hao, 2001) or a basal lycophyte (Kenrick & Crane, 1997, p. 176). The dimensions of spike, sporangia and stalks of the present specimen are in the minimum extreme of those of *H. gracilis* and are much smaller than those of *H. recurvata*. Sporangial stalks of specimen PKU-XH214, *H. gracilis* and *H. recurvata* are 2.0–3.9 mm, 4.0–13.0 mm (Wang & Hao, 2001) and 10–20 mm long (Geng, 1985), respectively.

It should be noted that the observed sporangial dehiscence in specimen PKU-XH214 is transverse, i.e. transversely dividing the sporangia on the adaxial face, which is different from dehiscence in *Huia gracilis*, which is reported to be longitudinal, along the radial plane of the fertile axis (Wang & Hao, 2001). Not considering the recurvation of sporangia, the transverse sporangial dehiscence is similar to that of most zosterophylls, such as *Zosterophyllum*, *Crenaticaulis* Banks & Davis, *Sawdonia* Hueber, *Discalis*, *Guangnania* Wang & Hao and others (Banks & Davis, 1969; Hao, 1989a; see fig. 4 in Gensel, 1992 and reference therein; Wang & Hao, 2002). In general, the characters of specimen PKU-XH214 indicate that the plant is most similar to the genus *Huia*, but it cannot be readily put into this genus, and thus is tentatively treated as aff. *Huia* sp.

4.c. Unnamed spike (Figs 4j, k, 5d, e)

A poorly preserved terminal spike was collected (PKU-XH215a, 215b, part and counterpart, shown in Figs 4j, k, 5d, e). The spike is 17 mm long and 5.2–7.2 mm wide, with an axis 0.8–1.4 mm wide, and bears at least nine helically arranged sporangia. The sporangia are ovate in side view, 1.6–2.4 mm wide and 2.5–3.7 mm high. The sporangial stalk is 0.6–0.9 mm wide and 1.6–1.9 mm long, with an acute insertion to the axis. Because of the fragmentary nature, an accurate taxonomic assignment of this specimen remains to be determined. The helically arranged stalked sporangia, however, indicate a probable zosterophyll affinity.

5. Composition of the Xitun flora

To date, plants reported from the Xitun Formation (the Xitun flora) include *Xitunia spinitheca*, *Zosterophyllum minorstachyum*, *Z. shengfengense*, Gen. nov. A, aff. *Huia* sp. and some unnamed spikes (Xue, 2009; Hao *et al.* 2010; and this work), showing diverse morphologies of vegetative (e.g. branching pattern, roots) and fertile structures (e.g. sporangial shape and distribution). There are also some additional unnamed

ribbon-like axes (not illustrated) which can be assigned to the morphogenus *Taeniochrada* White. *Xitunia* has lateral stalked sporangia, indicating a probable zosterophyll affinity, although there are some spiny appendages attached on the sporangia. *Zosterophyllum shengfengense* was established on the basis of a completely preserved specimen (Hao *et al.* 2010), with numerous root-like axes forming one of the earliest known rooting systems. Gen. nov. A is clearly a zosterophyll. Aff. *Huia* sp. has adaxially recurved sporangia comparable to those of the genus *Huia* from Pragian sediments of Yunnan. Other than these tracheophytes, several presumed algal species were recognized on the basis of fragmentary specimens (Cai & Wang, 1995). The axes of *Uncatoella verticillata*, being considered a dasycladalean alga, are very common in this flora (Li & Cai, 1978; Kenrick & Li, 1998).

6. Early Devonian plants from other localities of South China

The earliest record of *Zosterophyllum* in South China is from the Yulongsi Formation (Hao *et al.* 2007), which is considered Pridoli in age (Cai *et al.* 1994). *Zosterophyllum xishanense* was described from the lower part of the Xiashancun Formation (Hao *et al.* 2007); Li & Cai (1977) described *Z.* sp. 2 from this formation, consisting of only two isolated sporangia. Possible spikes of *Z. myretonianum* were reported from the Guijiatun Formation (Li & Cai, 1977). The Xujiachong Formation has yielded a rich assemblage (Table 1), including *Z. longhuashanense* Li & Cai, *Z. spatulatum* Li & Cai, *Z. bifurcatum* Li & Cai, *Z. yunnanicum*, *Z. australianum*, *Huia gracilis*, *Hedeia sinica* Hao & Gensel, *Guangnania cuneata* Wang & Hao, *Drepanophycus qujingensis* Li & Edwards, *Bracteophyton variatum* Wang & Hao, *Hsüa robusta* and *Hsüa deflexa* (Li & Cai, 1977; Wang, Hao & Liu, 2002; Wang, 2007 and reference therein).

Many plants, most of which are endemic, have been reported from the Posongchong Formation of Wenshan (c. 240 km south of Qujing), southeastern Yunnan, interpreted as Pragian in age based on fish, spores, the biostratigraphic coefficient method and regional stratigraphic correlation (Hao & Gensel, 2001). The Posongchong flora includes 23 genera and 25 species (Table 1), representing one of the best documented floras of the Early Devonian.

Other localities within the Early Devonian are poorly constrained to a Pragian–Emsian age (Table 1). Li & Cai (1977) described *Zosterophyllum* sp. from the Banmandaodi Formation of Naxi, Yunnan, *Z. sinese* Li & Cai, *Z.* sp. a, *Z.* sp. b and *Z.*? sp. c from the Shiqiao Group of Cangwu, Guangxi, and *Z. dushanense* Li & Cai from the Bangzhai Formation of Dushan, Guizhou. *Drepanophycus spinaeformis* Goepfert, *Z. yunnanicum* and *Psilophyton* cf. *P. goldschmidtii* Halle were later added to the plant assemblages of the Bangzhai Formation (Cai & Wang, 1995).

The Pingyipu Formation at Yanmenba, Jiangyou, Sichuan, of probable Pragian to early Emsian age, yields abundant plant fossils, including nine genera and 14 species (Table 1): four *Zosterophyllum* species, *Hicklingia* cf. *H. edwardii* Kidston & Lang, *Oricilla unilateralis* Geng, *Eogaspesica gracilis* Daber, *Uskiella* Shute & Edwards sp., *Psilophyton* sp., *Drepanophycus spinaeformis*, *D. spinosus* Kräusel & Weyland, *D.* sp., *Sciadocillus cuneifidus* Geng and *Ampectosporangium jiangyouense* Geng (Geng, 1992a,b; Cai & Wang, 1995; Wang, 2007). The composition of this flora needs reinvestigation, because plants such as *Hicklingia* Kidston & Lang and *Oricilla* Gensel were originally found in Lower Devonian deposits of Europe and North America (Laurussian palaeocontinents) (Edwards, 1976; Gensel, 1982b), and their occurrence in South China requires confirmation. As an example, Xu & Wang (2009) reinvestigated the specimen assigned to *Leclercqia complexa* Banks *et al.* by Geng (1992a), and believe that it does not belong to *Leclercqia*.

7. Lochkovian floras of South China and palaeophytogeographical considerations

The Lochkovian floras of South China reported here and in previous studies (e.g. Hao *et al.* 2007, 2010; Xue, 2009) shed some light on the origin of Early Devonian plant diversity in Asia. The Lochkovian floras from the Xiashancun and Xitun formations share one genus, *Zosterophyllum*, with the Pragian Xujiachong and Posongchong floras. Aff. *Huia* sp. from the Xitun Formation is similar to *Huia*, a genus found in both the Xujiachong and Posongchong floras (Geng, 1985; Wang & Hao, 2001). Thus, the Lochkovian floras share some elements with younger floras, showing a continuation of floristics in this area. Nevertheless, a large gap, both taxonomically and morphologically, still exists between the Lochkovian and the Pragian floras in Yunnan (and South China), with the emergence of new characters (i.e. evolutionary innovations) and plant types (probably at class or order levels), such as megaphylls (*Eophyllophyton* Hao; Hao, Beck & Wang, 2003), and microphylls and sporophylls (*Zhenglia* Hao *et al.*; Hao *et al.* 2006), which are not yet clearly attributed to known Lochkovian antecedents.

An update to the Lochkovian megafossil database has been provided by Edwards & Wellman (2001, their table 2.2) and Edwards *et al.* (2001b, their table 2). The genus *Zosterophyllum* had a very wide distribution, from Lochkovian deposits in Wales, England, Scotland, Germany, Siberia, Australia, Spitsbergen and South China (Wellman *et al.* 2000; Edwards & Wellman, 2001 and reference therein; Hao *et al.* 2007, 2010; Xue, 2009), but not from contemporaneous sediments of western Gondwana (e.g. Paraná Basin, Brazil, and Precordillera, Argentina; Edwards *et al.* 2001b; Gerrienne *et al.* 2001). The Lochkovian flora of South China includes *Zosterophyllum xishanense*, *Z. minorstachyum*, *Z. shengfengense* (Hao *et al.* 2007,

Table 1. List of vascular plants reported from the Silurian–Lower Devonian deposits of South China

Lithological units	Age	Basis for age	Composition	Selected literature
Xiushan Formation (Guizhou)	Llandovery (early Silurian)	invertebrate faunas	<i>Pinnatiramosus qianensis</i>	Cai <i>et al.</i> 1996; but see Edwards <i>et al.</i> 2007
Yulongsi Formation (Yunnan)	Pridoli (latest Silurian)	conodonts, spores	<i>Zosterophyllum qujingense</i>	Hao <i>et al.</i> 2007
Xiaxishecun Formation (Yunnan)	early Lochkovian	spores, fish	<i>Zosterophyllum xishanense</i>	Hao <i>et al.</i> 2007
Xitun Formation (Yunnan)	mid–late Lochkovian	spores, fish	aff. <i>Huia</i> sp.; Gen. nov. A; <i>Xitunia spinitheca</i> ; <i>Zosterophyllum minorstachyum</i> ; <i>Z. shengfengense</i>	Xue, 2009; Hao <i>et al.</i> 2010; this paper
Guijiatun Formation (Yunnan)	late Lochkovian–early Pragian	spores, fish	<i>Zosterophyllum myretonianum</i>	Li & Cai, 1977
Xujiachong Formation (Yunnan)	Pragian–early Emsian	spores, fish, bivalves	<i>Bracteophyton variatum</i> ; <i>Drepanophycus qujingensis</i> ; <i>Guangnania cuneata</i> ; <i>Hedeia sinica</i> ; <i>Hsüa robusta</i> ; <i>Hsüa deflexa</i> ; <i>Huia gracilis</i> ; <i>Zosterophyllum australianum</i> ; <i>Z. bifurcatum</i> ; <i>Z. longhuashanense</i> ; <i>Z. spathulatum</i> ; <i>Z. yunnanicum</i>	Li & Cai, 1977; Li, 1982; Wang, Hao & Liu, 2002; Wang & Hao, 2004; Wang, 2007 and references therein
Posongchong Formation (Yunnan)	Pragian	spores, fish, biostratigraphic coefficient method (Gerrienne, 1996)	<i>Adoketophyton subverticillatum</i> ; <i>A. parvulum</i> ; <i>Baragwanathia</i> sp.; <i>Catenalis digitata</i> ; <i>Celathea beckii</i> ; <i>Cervicornus wenshanensis</i> ; <i>Demersathea contigua</i> ; <i>Discalis longistipa</i> ; <i>Eophyllophyton bellum</i> ; <i>Estinnophyton yunnanense</i> ; <i>Guangnania cuneata</i> ; <i>Gumuia zyzzata</i> ; <i>Halleophyton zjiichangense</i> ; <i>Hedeia sinica</i> ; <i>Hueberia zhichangensis</i> ; <i>Huia recurvata</i> ; <i>Psilophyton primitivum</i> ; <i>Polythecophyton demissum</i> ; <i>Ramofelis amalia</i> ; <i>Stachyophyton yunnanense</i> ; <i>Wenshania zhichangensis</i> ; <i>Yunia dichotoma</i> ; <i>Zhenglia radiata</i> ; <i>Zosterophyllum australianum</i> ; <i>Z. ramosum</i>	Hao & Gensel, 2001 and references therein; Hao, Wang & Wang, 2004; Hao <i>et al.</i> 2006; Hao & Xue, 2011; Yang, Li & Edwards, 2009; Zhu <i>et al.</i> 2011
Banmandaodi Formation (Yunnan)	? Pragian–Emsian	plants	<i>Zosterophyllum</i> sp.	Li & Cai, 1977
Shiqiao Group (Guangxi)	? Pragian–Emsian	plants	<i>Zosterophyllum sinense</i> ; <i>Z. sp. a</i> ; <i>Z. sp. b</i> ; <i>Z.?</i> sp. c	Li & Cai, 1977
Bangzhai Formation (Guizhou)	? Pragian–Emsian	plants	<i>Drepanophycus spinaeformis</i> ; <i>Psilophyton</i> cf. <i>P. goldschmidii</i> ; <i>Zosterophyllum dushanense</i> ; <i>Z. yunnanicum</i>	Li & Cai, 1977; Cai & Wang, 1995
Pingyipu Formation (Sichuan)	Pragian–Emsian	plants, fish	<i>Amplectosporangium jiangyouense</i> ; <i>Drepanophycus spinaeformis</i> ; <i>D. spinosus</i> ; <i>D. sp.</i> ; <i>Eogaspesia gracilis</i> ; <i>Hicklingia</i> cf. <i>H. edwardii</i> ; <i>Oricilla unilateralis</i> ; <i>Psilophyton</i> sp.; <i>Sciadocillus cuneifidus</i> ; <i>Uskiella</i> sp.; <i>Zosterophyllum myretonianum</i> ; <i>Z. sichuanense</i> ; <i>Z. yunnanicum</i> ; <i>Zosterophyllum</i> new species (Wang, 2007)	Geng, 1992a,b; Cai & Wang, 1995; Xu & Wang, 2009

2010; Xue, 2009), all having radially (or irregularly) arranged sporangia. Lochkovian species of *Zosterophyllum* found from the Lower Old Red Sandstones include *Z. myretonianum*, *Z. fertile* and cf. *Z. fertile* (Edwards, 1975; Wellman *et al.* 2000; Edwards & Wellman, 2001). *Zosterophyllum myretonianum* has both radially and bilaterally arranged sporangia, while *Z. fertile* bears sporangia in two rows. At this time, no species have been confirmed to be shared by South China and Europe, although Li & Cai (1977) reported two fragmentary spikes possibly assignable to *Z. myretonianum* from South China. Combining the evidence from Lochkovian and Pragian–Emsian floras, Hao *et al.* (2007) suggested that the zosterophylls with radially arranged sporangia were probably dominant in the early land floras of South China, while those with sporangia in rows were common in the Laurussian palaeocontinent. This suggestion is supported by the plants reported from the Xitun Formation.

The Lochkovian floras of Laurussia and western Gondwana, such as England (Edwards, Fanning & Richardson, 1994; Wellman, Edwards & Axe, 1998; Edwards & Wellman, 2001), Paraná Basin, Brazil (Gerrienne *et al.* 2001, 2006) and Precordillera, Argentina (Edwards *et al.* 2001b) are dominated by plants with isotomous branching and terminal sporangia, such as species of *Cooksonia* Lang, *Pertonea* Fanning *et al.*, *Isidrophyton* Edwards *et al.* and others. These plants share the same grade of organization (i.e. small size, isotomous branching and terminal sporangia; Gerrienne *et al.* 2001; Edwards *et al.* 2001b); however, their phylogenetic position, although difficult to determine owing to the morphological simplicity and the lack of anatomy, probably would be different. Some of them may be basal eutracheophytes, while others are assigned to polysporangiophytes (Gerrienne *et al.* 2001), or only to Plantae insertae sedis in taxonomy (Edwards *et al.* 2001b). On the contrary, no similar plants have been discovered so far from the Silurian–Lower Devonian deposits of South China. It seems that such kinds of plants were not dominant elements in South China. Furthermore, compared to the zosterophyll-dominated Lochkovian floras of South China, zosterophylls are significantly absent in the reported assemblages of Argentina and Brazil (Edwards *et al.* 2001b; Gerrienne *et al.* 2001, 2006). The global phytogeographic patterns of the Late Silurian recognized by Raymond, Gensel & Stein (2006), i.e. the North Laurussian unit (with Bathurst Island, near the palaeoequator), South Laurussian–Northwest Gondwanan unit, Kazakhstani unit and Northeast Gondwanan (Australian) unit, might extend into the Early Devonian. It is apparent that South China, geographically near the palaeoequator and phytogeographically part of the Northeast Gondwanan unit (see Hao & Gensel, 1998), supported floras different from those of the Laurussian and Gondwanan palaeocontinent, and that these differences can be traced to as early as the Lochkovian from the evidence of megafossil plants.

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