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Lower Devonian lycophytes from Sichuan and the palaeogeographic context of coeval plant assemblages from South China.

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Devonian plants from Sichuan

Abstract

- Premise of the Research

Devonian assemblages from South China have become an important source of data on the rise of land plants thus supplementary to a scenario historically based on fossils from the Laurussian region and Siberia. Less attention has been placed on assemblages from Sichuan compared with Yunnan and adjacent provinces of China, and their palaeogeographic significance.

- Methodology

Descriptions of plants with enations, including lycopsids, are based on coalified compression fossils lacking anatomy, and complete our analyses of the Sichuan Lower Devonian assemblages. Compiled species lists for the entire assemblage are compared with those from coeval assemblages from South China using simple statistical methods (including Simpson's coefficient of similarity)

- Pivotal Results

Studies confirm the presence of endemic lycophytes and emphasise the importance of detailed study of *Drepanophycus spinaeformis* before any conclusions on its global occurrence can be made.

- Conclusions

Statistical analysis of the whole flora confirms the distinctiveness of the assemblage from Sichuan from those of Yunnan, but the distinctiveness of two further subregions in South China requires further taxa to be described.

1. Introduction

Historically, the dominant source of knowledge of the Devonian rise of land plants has come from fossils discovered from the Laurussian region, particularly North America, Europe, the European Arctic and Siberia. More recently China, and particularly South China, has become an important source of data. The South China Continent lay close to the palaeoequator a long way from Laurussia (Torsvik and Cocks 2017), and therefore the differences between the Laurussian and South Chinese Devonian plant fossil assemblages have the potential to change our perception of plant evolution during this important time. In this paper we will concentrate on Early Devonian age plant assemblages from Sichuan Province, and compare them with other plant assemblages of an approximately equal age from Guangxi, Guizhou and Yunnan Provinces.

Previous descriptions and reinvestigations of the Lower Devonian assemblages in the Pingyipu Group, Jiangyou County, Sichuan (Geng 1992a,b; Xu and Wang 2009; Edwards, Geng and Li 2016; Edwards and Li 2018a,b) have confirmed the high degree of endemicity in Sichuan. Our recent studies concentrated on plants with smooth stems including (1) those with terminal sporangia related to the rhyniophytes (e.g. *Jiangyounia gengi*, *Polycladophyton gracilis* Edwards and Li 2018a), (2) those with sporangia aggregated into strobili belonging to the zosterophylls (*Guangnania minor* (Edwards et al. 2016), *Zosterophyllum ovatum*, *Ornicephalum sichuanense* (Edwards and Li 2018b), *Bauyinia sichuanensis*, *Sichuania uskielloides* (Edwards and Li 2018a)), (3) those where strobili contain bracts (barinophyte *Adoketophyton pingyipoensis*, Edwards and Li 2018b) as well as plants with highly branched terminal fertile complexes (*Amplectosporangium* species, Edwards and Li 2018b). *Yanmenia* (*Zosterophyllum*) *longa* is an exception because it comprised leafy plants reminiscent of lycopsids, but with no reproductive or anatomical characters that would allow unequivocal assignment to that lineage (Edwards et al. 2016). Here we reinvestigate the fossils originally placed in the genus *Drepanophycus* by Geng (1992a) and provide some further data on specimens originally named *Leclercqia* by Geng (1992a) that confirm the need for a different genus as was suggested by Xu and Wang (2009) on the basis of its highly dissected leaf tips.

The revised list of taxa indicates that, apart from *Zosterophyllum* and *Drepanophycus*, most of the genera noted in the Sichuan flora are endemic. This invites further consideration of the reasons for the distribution of the two disparate plant groups in China in addition to their relationships on a global scale in Early Devonian times.

2. Locality, stratigraphy and age

Assemblages have been collected from three horizons in roadside exposures in the lower part of the Pingyipu Group in the Tangwanzhai Syncline near Yanmenba, Jiangyou County, Sichuan (see Edwards et al. 2016, lithological log on p. 4). The plants described below with undivided leaves come from near the base of the sequence (Horizon 1), and the new taxon with much divided leaves (*Multapicifolium*) from near the top (Horizon 3). There is no direct, independent evidence for the age of the sequence, but it is estimated to extend from the Lochkovian to the upper Pragian. Horizon 1 is considered to be Lochkovian or possibly lowermost Pragian and Horizon 3, uppermost Pragian (Edwards et al. 2016).

3. Material and methods

Most of the plants are preserved as coalified compressions, but the coal has disappeared to varying extents. Where missing the exposed rock is slightly paler and flatter than the entombing matrix. All taxa with enations recovered from Horizon 1 are lycophytes, except for one where anisotomously branching slender stems, c. 1.0-2.0 mm diameter (Fig. 1a) bear narrow spines c. 0.5 mm long and 0.1 mm wide (Fig. 1b). It was figured by Geng (1992a, Plate 5, figs. 43, 44) and named *Psilophyton* sp., but in the absence of reproductive parts and anatomy is better named *Psilophytites* sp. (Høeg 1952). It indicates the existence of a grade of organisation, but has no systematic or palaeogeographical significance. The older fossils (Horizons 1 and 2) are preserved in a buff to grey, relatively soft silty sandstone. The rock in the upper horizon (3) is a darker grey and much harder, and the fossils more heavily coalified.

Examination under dissecting microscopes in Cardiff and Beijing was followed in Cardiff by photography with polarised light using a Nikon D800 digital camera, and for higher magnification a LEICA MZ 16 stereo microscope using Leica Application Suite (LAS) software. A similar system was used in Beijing. Neither anatomical data nor spores were revealed using Schultz solution.

All specimens are housed in the Palaeobotanical Museum of China, Institute of Botany, Chinese Academy of Sciences, Xiangshan, Beijing.

4. Fossils attributed to *Drepanophycus*

These include specimens described by Geng (1992a) as *Drepanophycus spinaeformis* (his Plate 6, 48, 49), *D. spinosus* (Plate 6, figs 50-52) and *Drepanophycus* sp. (Plate 6, figs 45-

47) as well as newly collected material. The specimens with markedly different leaf morphology named as *Drepanophycus* sp. will be considered later.

4.1. *Drepanophycus* cf. *spinaeformis* (Figs 1c, 2, 3)

Cursory examination of the specimens appears to indicate that two distinct taxa are present based on size, the larger named *D. spinaeformis* by Geng and the slenderer, *D. spinosus*. However, subsequent more detailed analysis shows that leaf morphology, viz narrow laminae tapering from a slightly decurrent base to a rounded acuminate tip producing a falcate profile (Figs 2a, b, e), is similar, while stem and leaf dimensions form a continuum. In both, branching is rare but either dichotomous (Figs 2d, 3d) or anisotomous having developed from lateral buds with crowded, shorter leaves (Figs 2f, 3h), these smaller leaves being confined to the base. Leaf arrangement cannot be determined as there is vertical overlap and even where leaf bases are seen in relief on stem surfaces (Fig. 2f), the area preserved is too short to determine phyllotaxis.

A prominent difference between Geng's two species relates to the amount of coalified matter remaining on the specimens. Thus considering the larger specimens, assigned to *D. spinaeformis* (Geng 1992a) and illustrated here (Figs 1c, 2a-d, 3e, g, h), the stems are broad and preserved as smooth impressions, a little darker grey than the surrounding matrix, with little or no coal remaining, this being largely confined to tips of leaves and presumed vascular tissues (Fig. 2a).

In those specimens with narrower stems, the smallest examples may be almost completely coalified with more or less continuous black, glassy surfaces (Fig. 3d). In others, including those named *D. spinosus* by Geng (1992a, Plate 6, figs 50, 52), the coal is sporadic, less cohesive and flaky, revealing the stained matrix below (Fig. 2f) or almost completely absent (Fig. 2e). Leaves appear more crowded on the narrow stems of this second group, but dimensions (Table 1), while differing in their means, show small overlap in their ranges. This, plus leaf morphology, leads to the conclusion that all the specimens are conspecific, the smaller (Type 1 here), in some instances possibly representing distal parts of the plant. Indeed, a number of specimens with truncated ends perhaps represent apices (Figs 3c, d) and a similar termination with crowded needle-like leaves was illustrated by Geng (1992a, Plate 6, fig. 51). It was thought to bear circular sporangia, 0.3 to 0.35 mm in diameter, directly attached to the stem.

A unique specimen, preserved as part and counterpart, in demonstrating the two preservation forms, offers an alternative explanation for the difference. One has abundant coalified material (Fig. 3b) and the other is essentially an impression with the coalified material concentrated in vascular strands and leaves (Fig. 3a). In the latter, it resembles the condition in the wider stems, where the longitudinally running, usually centrally placed vascular strands are remarkably consistent in diameter (<0.8 mm). However, it seems unlikely that all the wider illustrated examples are counterparts. Perhaps more likely taking into account the size differences, in the wider forms originally coalified material was dislodged during collection, subsequent transport and storage.

Vasculature. As noted above, a conspicuous feature of the wider stems is the longitudinally orientated strip of coalified material interpreted as the remains of vascular tissues (probably xylem). Slightly narrower are the lateral traces that depart at an acute angle (Fig. 2a) and remain within the ground tissue for some distance before entering the base of a branch (Fig. 2d) or lateral bud (Fig. 3h – white arrow). Even narrower but shorter strands depart at a narrow angle and end in lightly coalified circular areas (Figs 2c - arrow, 3e, h – black arrow). The latter are interpreted as sporangia where sporopollenin might be more resilient to decay. Such an interpretation would explain the observation that lateral traces are far more abundant than branching.

Throughout this investigation, it has been assumed on comparative morphological grounds that the enations/leaves are microphylls, but apart from very faint, longitudinally orientated lines in the ground tissue (Fig. 1c - arrows), there is no convincing evidence for leaf traces, their absence probably indicating their slender nature when compared with traces to branches and sporangia.

The fossilisation of the strand suggests that its tissues were more resistant to decay than those of the ground tissues, be they parenchyma or aerenchyma. Displacement of the stem traces (Fig. 3g) is considered to result from the probably rapid decay of these extraxylary tissue resulting in compression of an essentially empty cuticularised cylinder. This was postulated by Hueber (1992) for both *Drepanophycus* and *Asteroxylon.*

4.2. Identification

Lycopsids with simple leaves in the vegetative state and lacking anatomical detail are notoriously difficult to identify. From leaf shape and branching patterns, the above specimens are concluded to belong to the genus *Drepanophycus.* Again, on morphological grounds and distribution of leaves, they resemble *D. spinaeformis* which, as evidenced from the specimens illustrated by Li et al. (2000) in their distinction of the neotype from an extensive Emsian assemblage from New Brunswick, display considerable variation in form and preservation. However their circumscription of the species included leaf shape, orientation and vascularisation, stomatal characters, stem anatomy and cauline sporangia. The Sichuan specimens resemble *D. spinaeformis* on vegetative morphology, but no further diagnostic characters, not even microphylls, have been demonstrated. Considering the characteristics of the remaining then adequately known species, Grierson and Hueber (1967) concluded that *D. spinaeformis* could be distinguished from other species such as *D. gaspianus, colophyllus* and *eximus* because it possessed 'loose spiral to irregular' leaf arrangement, as is seen in the Sichuan specimens. We reject Geng's placing some of the specimens in *D. spinosus* and agree with Grierson and Hueber (1967) that this Middle Devonian taxon (Kräusel and Weyland 1933) 'may prove to be several species or even genera'. Nevertheless, we cannot be certain of their assignation to the type species. We faced a similar dilemma when we erected a new species, *D. qujingensis* from Yunnan (Li and Edwards 1995), on the basis of leaf orientation, potentially a taphonomic effect, and stomatal characteristics, the latter impossible to distinguish in the Sichuan coalified material where cuticles are lacking. However Li et al. (2000) questioned our decision that was largely based on stomatal apparatus. Thus, as a consequence of this dearth of characters, we choose to emphasise uncertainty by the use of the species prefix cf.

4.3. Drepanophycaleans in the Chinese Lower Devonian

Although we cannot be certain that *D. spinaeformis* existed in Sichuan, it is of some interest to explore its distribution in the Chinese Lower Devonian. Surprisingly, neither *Drepanophycus spinaeformis* nor *D. qujingensis* is recorded in the Posonchong Formation, but vegetative fragments of a putative drepanophycalean, *Hueberia zhichangensis* (Yang, Li and Edwards 2009), have been found in the Formation near Zhichang village, south of Wenshan. The stems, up to 1.8 mm wide, branch isotomously and presumed distal upright parts bear falcate enations arranged in a regular helix with 6 to 8 per gyre. The enations are 0.6 - 1.0 mm wide and 0.9 – 1.6 mm long.

The original description of *Hueberia zhichangensis* Yang, Li et Edwards (2009) was based on only two specimens from from the Posongchong Formation of Wenshan. Xue (2013) described an extensive assemblage of *Hueberia zhichangensis* and has provided further information on gross morphology including buds, sporangia and the interpretation of basal smooth axes as rhizomes. Most importantly, he illustrated vascular strands in stems and lateral appendages, thus confirming them as microphylls and allowing assignation to the lycophytes. In a comparative list including global coeval representatives, he included *Drepanophycus qujingensis* (Li et Edwards 1995) from the same area but rejected relationship on the basis of the latter's greater dimensions in axial width, and absence of its anatomical distinguishing features. Such differences would also apply to comparisons with *Drepanophycus spinaeformis*, not recorded in the same formation. Since size is not a satisfactory criterion for distinction of species, there remains the possibility that *Hueberia* might be congeneric with *Drepanophycus.* Only the discovery of anatomy will resolve this enigma.

Drepanophycus qujingensis Li et Edwards from the Xujiachong Formation in Zhanyi County, Qujing, Yunnan was originally described as *D.spinaeformis* by Halle (1936) from the then named Longhuashan Formation and subsequently noted as *D. spinaeformis* by Li and Cai (1978). As mentioned above, Li and Edwards (1995) erected a new species on this material from leaf orientation, stomatal anatomy and reproductive characters.

Liu et al. (2004) had reported the genus from ten horizons in the Xujiachong Formation in Yunnan including *D. qujingensis*, with no detailed descriptions, and a fertile record of *D. spinaeformis* from Dushan (Fig. 4), Guizhou Province (Geng and Zhu 1994) was also considered to belong to *D. qujingensis* (Li and Edwards 1995). The same assignation might be appropriate for leafy stems placed in *D. spinaeformis* and two new species of *Drepanophycus* also from the Xujiachong Formation, as well as *D. spinaeformis* from the underlying Guijiatum Formation (Fang et al. 1985). Further afield (see Fig. 4), the latter has been recorded at Cangwu in the Shiqiaopo Group, in eastern Guangxi, at Lijiang, Yunnan, in the Banmandaodi Formation, in and in clastic rocks in the Changning area of western Yunnan, which was possibly part of the Shan-Thai palaeocontinent (Cai and Wang 1995, Domeier 2018). All these Chinese occurrences of *D. spinaeformis* require further investigation and validation before they can be considered unequivocal records of the type species. Such caution is essential before phytogeographic analysis as it would be the only cosmopolitan species in the Early Devonian flora of the South China plate.

4.4. Global distribution of *Drepanophycus spinaeformis*

Numerous records of *D. spinaeformis* occur from Lochkovian to Emsian localities on both European and north American areas on the palaeocontinent Laurussia. Li et al (2000) set the standard for unequivocal identification of the species in their circumscription of the neotype based on New Bruswick material, which includes morphological, anatomical and reproductive data. The latter were missing from Scottish Emsian material (Raynor 1984), while other records are based variably on gross morphology, including branching and roots, epidermal anatomy etc. (e.g. Gensel et al. 2001). Thus plants with falcate leaves, some assignable to the type species with confidence, certainly grew in North American and Scottish Laurussia, and probably elsewhere in Europe.This, taking Chinese records into account, makes *Drepanophycus* a rare example of a cosmopolitan genus in Lower Devonian times. However we cannot accept *Drepanaphycus spinaeformis* as a cosmopolitan species without further scrutiny.

5. Other specimens attributed to the genus *Drepanophycus* by Geng (1992a) Fig. 5

Geng illustrated four fragments (1992a; plate 6, figs 45-47) named as *Drepanophycus* sp. Of these, the longest (120 mm) is unbranched, and the better, more completely preserved example also illustrated here (Fig. 5), bifurcates at the base and is c. 94 mm long. The leaves are roughly triangular in outline with their long axes almost perpendicular to the stem, except for two close to the branch point, where the lamina is slightly reflexed. Leaf bases are slightly decurrent and tips rounded. They are 6.1-9.0 mm long ($\bar{x}$ = 6.4, n = 100) and 5.9-7.9 mm wide at base ($\bar{x}$ = 6.2, n = 10). The surfaces of the regularly inserted leaves are continuous with that of the stem suggestive of attachment on its side, although the base of a few demonstrate that insertion is three-dimensional. Some are indicated by a crescent - shaped depression (Fig. 5c - black arrow) and others are ‘behind’ the axis (Fig. 5b – black arrow). Thus leaf arrangement is equivocal. The surface of the specimen illustrated here show longitudinal, irregular ridging, which extends onto the basal regions of the leaves. Figure 5b also shows leaves where a very straight, narrow, linear structure emanating at right angles from the stem extends into the lamina (white arrows), a further example enlarged in fig. 5c (white arrow). This is interpreted as a leaf trace, but while a narrow, central longitudinally orientated strand is clearly illustrated by Geng in the centre of the axis on the same specimen, it is less apparent under our dry, cross polar photography.

Identification Triangular vascularised enations are interpreted as microphylls, with the inference of a lycopsid affinity and probably within the Drepanophycales, but in the absence of anatomy and fertile organs is better left as *Incertae sedis*.

6. Specimens attributed to *Leclercqia* (Geng 1992a; plate 7, figs 62-64) Figs 6, 7

6.1. Description

Geng illustrated two specimens, a 295 mm long well-preserved stem with many leaf bases and laterally compressed leaves, and a shorter specimen in which one of the leaves, showing a division into at least four segments, was the most prominent preserved feature. Macerated leaf fragments (Geng 1992a, Plate 8) suggested at least six segments. Reinvestigation of the longer specimen (specimen 8355; Geng 1992a, Plate 7, fig. 64) by Xu and Wang (2009) has shown that doubts concerning the identification of the leafy lycophyte as *Leclercqia* (Cai and Wang 1995; Hao and Gensel 2001; Xu and Wang 2009; Hao and Xue 2013) were justified as evidenced by their description of a leaf which comprised at last 12 distal segments. They were able to show, following removal of several layers of sediment around a laterally compressed leaf, that the segments were preserved at different levels, and that 'lateral' ones appeared shorter but there was no obvious recurved central segment, the presence of such a central segment being characteristic of the five to at least seven tipped leaves of those species of *Leclercqia* with three dimensional leaves (e.g. Banks et al. 1972; Xu et al. 2011). Xu and Wang (2009) considered an incomplete 'oval-elongate' structure (c. 1.3 mm long, 0.8 mm high) a sporangium which was adaxially attached halfway along the proximal undivided part of an unmodified leaf.

We here illustrate the smaller specimen (specimen 8354; Geng 1992a, Plate 7, figs 62, 63), which was not studied by Xu and Wang, including the small cluster of segments terminating the leaf (Fig. 6d, e), which led Geng to suggest identity with *Leclercqia*. It differs from the longer specimen, by longer leaf length before division (c. 4.0-4.3 mm v 2.5-2.7 mm) in its smaller diameter (c. 8 mm v. 11.3-12.1 mm), and probable fewer leaves per gyre.

In both specimens, where the leaves are observed beside the stem, they are inserted perpendicularly to about 45° above the perpendicular, and are slightly to moderately curved adaxially.

Xu and Wang (2009) concluded that additional information was needed before naming the specimens, although they appreciated their distinction from other Devonian lycophytes with divided leaves.

During the course of our reinvestigation of the assemblage from Horizon 3 in which we described the new zosterophyll, *Guangnania minor* (Edwards et al. 2016), we discovered a third occurrence of the lycophyte close to the strobilus. Alongside a compressed relatively narrow stem (2.1 mm diameter) with a typical proximal part of a leaf, is a further unusually preserved stem which is compressed flat, but oblique to the slab surface, appearing as an almost linear feature (Fig. 6a). It bears on both sides vertically compressed basal regions of leaves, the most completely preserved numbering ten with a further three attached on part of the stem inclined to the rest. Two of the leaves appear more or less complete (Fig. 6b). The base of the lamina is 0.25-0.35 mm wide, and narrows gradually proximally and then to a gentle taper distally. Its minimum width of 0.22-0.25 mm is some 1.7-2.0 mm from the base. The end of the lamina forms a broad expanded area, 0.4-0.5 mm wide and about 0.4 mm long. The numerous distal segments emerge perpendicular to the margin of the expanded termination of the lamina to form a broad fan, including some of which appear to point obliquely back towards the stem. The total number of segments is up to 15, of approximately equal length and width. The individual segments are 0.04-0.06 mm wide at the base, and up to at least 0.75 mm long, tapering over their entire length. No branching of the segments has been observed.

The overall three-dimensional arrangement of the segments at the end of the lamina is hard to interpret from the limited number of compressions that have been examined. In face view the segments seem to form a continuous fringe of non-overlapping segments which are divergent distally. In lateral compression, which is presumably partially oblique after impact with the sediment during preservation, the arrangement is more complicated (e.g. Geng 1992a Plate 7, fig. 63; Xu and Wang 2009). Geng (1992a, Plate 8) illustrated 3-D leaf fragments obtained by maceration, which suggest that the termination of the leaf petiole was a broad structure which had an oblique flat surface sloping in towards the ?adaxial surface of the leaf, and that the segments were arranged around this except where that surface intersected the adaxial surface of the lamina proximally.

A fourth specimen (Fig. 6c) from the horizon comprised a poorly preserved axis with jumbled mass of leaves, lacking terminal features. Among them are some darker patches, with irregular patches which may represent sporangia, but indicate little or no distinct shape or attachment.

Our reconstruction of the leaf of *Multapicifolium*, summarising our interpretations of the above descriptions, is presented in Figure 7.

6.2. Identification

Although none of the specimens show definitive phyllotaxis, the regularity and density of leaf insertion along the margins of the compressed axes is exactly as expected of a small herbaceous lycopsid. This is supported by the probable partially preserved adaxial sporangium illustrated by Xu and Wang (2009).

In the Early Devonian of South China, small, probably herbaceous, lycophytes are known from Yunnan but have undivided leaves. Two of these, *Zhenglia* (Hao et al. 2010) and

Halleophyton (Li and Edwards 1997) have obvious rhomboidal leaf bases. Others are more similar to the *Drepanophycus* forms described above.

Herbaceous lycopsids with divided leaves and small leaf bases generally belong to the Protolepidodendrales. The best-known Early Devonian forms are those of *Leclercqia andrewsii* from the Emsian of Maine (Gensel and Kasper 2005). These terminate in five quite broad segments, of which the central one is the broadest and longest, the overall shape being planate.

Of Middle Devonian Protolepidodendrales, those leaves that divide into segments are generally 3-tipped (genus *Colpodexylon* Banks 1944), or 5-7 tipped (genus *Leclercqia* Banks et al. 1972). In both forms the central segment is the largest. In Middle Devonian *Leclercqia* the central segment is usually abaxially recurved, and the lateral segments are arranged on either side in distinctive three-dimensional subunits which are not the result of dissection of a flat structure. In *Colpodexylon*, the leaf is essentially a dissected flat leaf.

In South China there is an endemic protolepidodendralean, *Minarodendron* Li (1990), in which the three segments are not arranged in a single plane, but the central tip, which is not enlarged, is abaxially recurved (Liu et al. 2013).

If the identity of the new plant as a protolepidodendrid is correct, it is unique in that it has a lamina which is dissected into a very large number of approximately equal segments, lacking a large central segment. This is very distinctive. It is possible to envisage how this relatively early form might have evolved into the later forms of Protolepidodendrales as summarised above.

Considering alternative affinities, intriguing potential early sphenophylls have been reported from Yunnan including *Estinnophyton yunnanese* Hao et al. 2004 and *Cervicornus wenshanensis* Li et Hueber 2000. *Estinnophyton* has very slender leaves which are dichotomised twice, including near the base, and has two sporangia attached near the second dichotomies. *Cervicornus* is similar but has a third dichotomy meaning that there are eight terminal segments. Although the overall appearance of *Cervicornus* is superficially like the new plant, the detail of how the several slender segments are derived is different – rather than arising from a flat spoon-shaped termination of a lamina, it is achieved by multiple dichotomies, and the leaves have a deep medial dissection. Furthermore, leaves are much more sparsely arranged in whorls. It is very unlikely that the new plant is allied to either genus and hence the sphenophylls.

6.3 Systematics

Class Lycopsida *sensu* Hao and Xue 2013

Order Protolepidodendrales

Family Incertae sedis

Genus Multapicifolium *Edwards, Li et Berry gen. nov.*

Generic diagnosis. Small lycopodiaceous plant with densely inserted microphylls. Microphylls, inserted at 45°, have a narrow lamina which broadens slightly distally to form a circular to oval termination, from the margin of which up to at least 15 equally spaced very slender segments diverge in a digitate, radiate arrangement in all directions except backwards parallel to the laminae, and are of approximately equal length.

Derivation of name. From the latin; *multus* (many, numerous), *apex* (tip), *folium* (leaf).

Type. *Multapicifolium sinense* gen. et sp. nov.

Multapicifolium sinense *Edwards, Berry et Li sp. nov.*

Diagnosis (based on Xu and Wang 2009 and this work). Axes 8-13 mm diameter, bearing leaf attachments which appear to be helically inserted. Leaf lamina 0.25-0.5 mm wide, 2.5 - 4 mm long before division. Distal segments 0.04 - 0.06 mm wide, and up to 0.9 mm long with fine (subulate) tip. Probable sporangium oval-elongate, c. 1.3 x 0.8 mm on isomorphic sporophyll.

Holotype: Palaeobotanical Museum of China, Institute of Botany, 9291a (figs 6a, b)

Locality of holotype: Yanmenba section, Jiangyou District, North Sichuan.Stratigraphy and age: Horizon 3 in upper part of the Yanmenba section, Pingyipu Group, Tangwanzhai Syncline; uppermost Pragian (Edwards et al. 2016).

Etymology: from China.

7. Summary of taxonomic revision of the Sichuan assemblages

This paper concludes taxonomic revision of the Sichuan Lower Devonian plant fossil assemblages (Edwards et al. 2016, Edwards and Li 2018a, Edwards and Li 2018b, this paper), based on the original study by Geng (1992a, b) and original field work. These revisions are summarised in Table 2.

8. Discussion

8.1. Lower Devonian palaeogeography and geological history

Figure 8 shows a reconstruction based on Torsvik and Cocks (2017) of palaeocontinents at 410 million years, which emphasises the distribution of the four major land masses, viz. Gondwana, Siberia, North China/Tarim and Laurussia. Other plate reconstructions show some variation, e.g. in the position of Siberia (e.g. Scotese and McKerrow 1990) and the orientation of the South China plate (e.g. Fig. 5.5 based on Boucot et al (2009) in Hao and Xue (2013)). All indicate that the South China plate, united with Annamia (Indochina), was situated at the northern margin of east Gondwana within the tropics (Bai and Bai 1990). Earlier in the Palaeozoic, indeed even in Proterozoic times, these areas, based on palaeomagnetic and faunal evidence, were attached to the northeast Gondwana Himalayan – west Australian region (e.g. Metcalfe 2013). Cambrian and Silurian palaeomagnetic data (Yang et al. 2004, Huang et al. 2018) are considered to indicate juxtapositioning of South China with northwest Australia, although other reconstructions show intervening terranes (e.g. Sibumasu, Qiangtong (Metcalfe 2011, Cocks and Torsvik 2013)), but whether those formed emergent land masses cannot be determined. However in the Late Silurian – Early Devonian, rifting and separation of South China plate (and arguably Annamia) represented the early stages of the formation of the Palaeo-Tethys ocean. Thus began the separation of the present South China plate from Gondwana (e.g. Domeier and Torsvik 2014: Fig. 4), with its isolation established by the end of the Middle Devonian, as evidenced by the presence of endemic freshwater fish. Today, the South China Continent (SCC), based on tectonic, lithological and biotic features is one of the 11 regions of China. It is further subdivided into two former Precambrian cratons, the Cathaysia block and the Yangtze block (Domeier 2018), separated by a complex of faults paralleling the Chenghou-Linwu—Jiangshan-Shaoxing faults (Fig. 4). These faults and associated sedimentation evidence ongoing movement between the blocks during and after union in the early Neoproterozoic and up to the Late Palaeozoic, including the formation of a rift basin (Domeier 2018). The outer margins of the Yangtze block have been impacted by numerous orogenic events associated with the assembly of Asia. Of relevance to this study is the present day northeastern margin (Longmenshan) and the southeastern margin (bordering Vietnam), as seen in figure 4, and in figure 8 (*S* and *Y*).

During the Devonian marginal siliciclastics to shallow marine carbonates were deposited on a passive margin on the present northeast of the Yangtze block. During the complex regional collision of many plates starting in the Triassic (the Indosinian orogeny), an ocean basin filled with a thick sequence of turbidite deposits was squeezed between several continents to form the Songpan-Ganzi Fold Belt. This shortening thrust the passive margin sediments, including the Devonian sediments onto the Yangtze block in a series of parallel thrust faults which make up the Longmen Shan Thrust Belt (Yong et al. 2003). The plant localities in this paper occur on the eastern margin of the mountainous belt to the west of the Jiangyou-Guangyuun fault (Li et al 2010, Fig. 4) in the Tangwangzhai Nappe.

The origin of the southwestern margin of the Yangtze block is similarly complex, particularly its relationship to Indochina. The established view has been that much of Yunnan and north Vietnam were part of the Yangtze block during the Early Devonian (e.g. Gonez et al. 2012). Cai and Zhiang (2009) proposed the presence of a Dian – Qiong suture running near the border of Yunnan and Vietnam (Fig. 4), with the implication that southern Yunnan and north Vietnam would have been parts of the Indonesia plate during the Early Devonian. This has been challenged by Lehrmann et al. (2015), based on the presence of Triassic carbonate platforms.

8.2 Comparison of composition of Sichuan assemblages with those elsewhere in South China

The South China plate has been divided into various subregions, each said to possess a distinctive flora (Fig. 4; Ma et al. 2009; Wang et al. 2018). These were the Longmenshan (Sichuan) subregion, the Yunnan subregion, and the Guanxi (Cathayan) subregion. The principal locality in Longmenshan is near Yanmenba (Fig. 4; *4*). The principal localities in the Yunnan subregion are around Qujing (Fig. 4; *1*) and, assuming that the Dian – Qiong suture did not exist, most probably around Wenshan (Fig. 4; *2*) and Dô Son, Vietnam (Fig. 4: *5*) (Janvier et al. 1987).

More recently a further phytogeographic subregion was recognised, the Guizhou subregion (Wang et al. 2022), to the north east of Yunnan and to the north west of Guanxi. The main localities are at Hezhang and Dushan (Fig. 4). Like the Gangxi region, only a small number of taxa are present (6), and require further investment in collecting and revision. Therefore we do not emphasise these two subregions in the following analysis.

Considering the Longmenshan subregion, assemblages from Yanmenba (Fig. 4; *4*) summarized in this paper now contain 17 taxa in total (Table 2), with 12 well constrained genera and 14 species. Eight genera are endemic to the subregion (Table 3), and two others are otherwise present only in the Yunnan subregion (Qujing and Wenshan areas, Fig. 4; *1* &

2). *Zosterophyllum* (represented by two species, one endemic to Longmenshan, one also found in Qujing and Guizhou) and *Drepanophycus* are cosmopolitan genera – the latter possibly including the only cosmopolitan species in Longmenshan, and considered here *D.* cf. *spinaeformis*.

Here we analyse separately the species lists from the Wenshan and Qujing areas of the Yunnan region as they differ markedly in diversity and disparity (Table 3). The Posongchong Formation in Wenshan (Fig. 4; *2*) shows a very high degree of endemism amongst the over thirty taxa recorded (Hao and Xue (2013)). 15 genera are confined to the area, while *Guangnania* also occurs in both Longmenshan and Qujing, *Adoketophyton* with the former and *Huia* with the latter. *Demersatheca* and *Pauthecophyton* also occur in Guizhou. Cosmopolitan genera and those found elsewhere include *Baragwanathia* (Laurussia, Australia), *Zosterophyllum* (Laurussia, Australia), Yarravia (*Hedeia*) (Australia), *Estinnophyton* (Laurussia), *Psilophyton* (Laurussia), *Distichophyton* (Laurussia), and *Oricilla* (Laurussia), although the last two genera require re-evaluation. By contrast the assemblages near Qujing (Fig. 4 - *1*) are impoverished. There are two endemic genera, *Bracteophyton* and *Hsua*, confined to the region, while *Demersatheca, Huia* and *Guangnania* are shared with Wenshan — the latter genus also occurs in Longmenshan. The two cosmopolitan genera are *Drepanophycus* (*D. qujingensis*) and *Zosterophyllum (Z. yunnanicum* and *Z. australianum*--the former species shared with Wenshan and the latter shared with Australia).

The plants from Cangwu, Guangxi subregion (Fig. 4; *3*) are less well studied, and include *Changwuia* (Hilton and Li 2000) otherwise only found in the Guizhou subregion, an endemic species *Zosterophyllum sinense* (Li and Cai, 1977, Wang et al 2018), *Drepanophycus* cf. *spinaeformis* and an unnamed rhyniophytoid (Cai and Wang, 1995, Xu et al 2015). The flora from the new Guizhou subregion (Fig. 4 – Hezhang and Dushan) also include *Changwuia* and species of two Yunnan genera, *Demersatheca* and *Pauthecophyton*. Cosmopolitan genera include two species of *Zosterophyllum*, and perhaps *Drepanophycus* (Wang et al. 2022).

Table 3 tabulates some of the numerical results from our analysis. Longmenshan has a high percentage of both local (67%) and South China (83%) endemic genera, based on a total of 12. Wenshan has slightly lower numbers at 52% and 72%, but based on a much higher number of genera overall (29). Qujing has few genera (8) and the percentage of endemics is much lower (63% Chinese and only 25% local endemics). Pairwise comparison of Simpson’s coefficient of similarity show that the most closely related localities based on genera are unsurprisingly Wenshan and Qujing (63%), but Qujing is slightly more similar to Longmenshan (38%) than Wenshan is to Longmenshan (25%), perhaps reflecting distance.

While Chinese phyto-endemicity is usually attributed to its palaeogeographic isolation in the Devonian (e.g. Hao and Beck 1991a, b; Li and Edwards 1992; Hao and Gensel 1998), the differences in assemblages on the South China plate itself, particularly between the Longmenshan and Yunnan floras demand further explanation, as do those between Wenshan and Qujing. Those between Guangxi and Yunnan are explained by the presence of an epicontinental sea between them for long periods in the Palaeozoic (Wang et al. 2018), although scrutiny of the limited species lists suggests that the recognition of a distinct phytogeographic unit is premature.

8.3 Possible reasons for differences in flora between Yunnan and Sichuan

8.3.1. Hypothesis 1. Geographic isolation in the Silurian-Lower Devonian.

Today the Longmenshan and Wenshan localities are some 1,000 km apart. It is likely that thrusting and crustal shortening during the Indonesian orogeny has reduced this distance considerably. Qujing localities are c. 250km to the north of Wenshan, and therefore closer to Longmenshan.

While during the early part of the Silurian Yunnan and Sichuan were separated by shallow epicontinental seas (Rong et al. 2003), during Wenlock and Ludlow times the majority of the South China plate was land connecting the Yunnan and Sichuan areas. During the Early Devonian, shallow seas again began to encroach onto the continent, and the area around Yunnan was left a peninsula (Cai and Zhang 2009). Topography of the land between Yunnan and Sichuan localities included mountains and plateaux interpreted to be up to 3000 m above sea level (Fig. 6 of Edwards et al. 2016, and references therein).

The overall picture is of a reasonably sized continent (at least 1,000 km x 2,000 km) with considerable topography and varied shoreline, straddling or near the equator (Fig. 8).

A modern analogue for the Devonian South China area in terms of size and topography might be Borneo (approx. 1,200 x 1,100 km). Here, complex interaction of prevailing winds, monsoon, topography and geology lead to the presence of vegetation as varied as tropical rainforest, heathforest and savanna. In our reconstruction Yunnan assemblages would be closer to a coastline as is recorded by the differences in facies. Indeed Hao and Xue (2013) considered that Wenshan's position 'relative to the sun (illumination) and the possible inference of ocean currents' are characteristic of the hot and humid tropical climate in the equatorial zone today, whereas the slightly younger sediments were deposited on a presumed delta plain with palaeosols in which calcretes indicated strongly oxidising conditions and high evaporation rates usually indicative of arid climates (Boucot et al. 1982, Wellman et al. 2012). Thus we conclude that geographic isolation with topographic barriers and potentially climatic influences might account for the differences in composition.

8.3.2. Hypothesis 2. Habitat heterogeneity here combined with climate.

In this second scenario, in which Longmenshan had been attached to the South China plate since Proterozoic times, and enjoyed an assumed similar climate regime with no major physical barriers between the Yunnan and Sichuan localities, habitat heterogeneity is proposed as a possibility for differences between the assemblages. Hao and Xue (2013) in their comprehensive review of taxa in the Posongchong Formation in Yunnan noted local regional variation in composition of assemblages which they concluded, since climate was generally similar, resulted from variation in habitats. They illustrated this via a combination of facies data (indicative of palaeoenvironments), taphonomic analyses and species lists throughout two well exposed sections with abundant plants, the Zhichang and Changputang, in the Wenshan area, where only one assemblage was common to both.

In the Zhichang succession, near channel overbank environments with periodic, flooding contained a mixture of taxa and showed high diversity, but only a few dominant species in abundance. In Changputang, where environments were quieter with deposition on flood plains or marshes, some habitats nearer the coastline were characterised by monospecific stands. Such differences and exceptional diversity were attributed to the regional complex topography, yielding various habitats, and the possible inference of ocean currents (Hao and Xue 2013) as characterise the hot and humid tropical climate in the equatorial zone today.

By contrast the possibly slightly younger Xujiachong Formation recorded in Qujing, some 250 km to the north, comprised fluvial sediments deposited on a presumed delta plain with phases of aridity. Megafossil assemblages were described as monotonous containing the cosmopolitan genera *Zosterophyllum*, *Dawsonites/Psilophyton* and *Drepanophycus qujingensis*. In a broader analysis, Wang et al. (2002) suggested that the typical marine to continental sediments of the Xujiachong Formation, preserved an impoverished vegetation, including plants like *Drepanophycus* with sprawling growth habit, compared with the more diverse assemblages preserved in the mainly clastic continental rocks of the Posongchong Formation which were deposited in flooded areas near lakes and lagoons.

Similar approaches on habitat heterogeneity/niche partitioning in north-east Canada also produced equivocal results. Hotton et al. (2001) had demonstrated habitat partitioning in Emsian assemblages from the Gaspé, but Kennedy et al. (2012) describing the same taxa of similar age from New Brunswick found no evidence of 'persistant associations of taxa in particular sedimentological contexts'.

In Sichuan similar analyses are premature. Assemblages are few and detailed sedimentological data do not exist. However in view of the very few taxa in common with Yunnan, it seems unlikely that environmental critera alone could account for the differences in composition.

8.3.3. Hypothesis 3. Comparative ages of assemblages.

It could be argued that, however rigorous, the scrutiny of species lists in detecting comparative differences in diversity and disparity at times of rapid evolutionary change as occurred in early tracheophyte evolution, the outcomes are of limited value in the absence of precise dating of assemblages—dating that should be based on independent evidence utilising biostratigraphically useful indicator fossils.

In all South China subregions, plants have been dated using regional stratigraphic correlation and /or better dated formations above and below them (e.g. Pragian–Emsian but not younger than late Emsian Cangwu Formation of the Guangxi (Cathayan) subregion (Xu et al. 2015)) and occasionally involving palynological data. In some cases, spores have allowed both regional correlations and comparisons with the zonation of Laurussia (e.g. the ? early but not earliest Pragian to the earliest Emsian *polygonalis-emsiensis* Spore Assemblage Biozone of Richardson and McGregor (1986) in the Posongchong and Xujiachong Formations (Wang 1994; Wellman et al. 2012 respectively).The Posongchong Formation is overlain by strata containing upper Pragian conodonts. These Yunnan assemblages might be slightly younger than the assemblages at the base of the Pingyipu Group in the Longmenshan which has been dated as probably Lochkovian but extending into the Pragian by fish and spores, the latter identified to species level at another exposure. In the Yunnan subregion, the Xitun Formation underlying the Xujiachong Formation near Qujing has been dated as mid-late Lochkovian on the basis of invertebrates, fish and spores, the latter from the *newportensis- micrornatus* and *breconensis- zavallatus* Spore

Assemblage Biozones (Cai et al. 1994) and thus is possibly coeval with or slightly older than the basal Sichuan assemblages. Xue (2011) noted that the Xitun flora was dominated by zosterophylls, but apart from the genus *Zosterophyllum*, it has no taxa in common with Sichuan. Thus on age, while there remains the possibility that the Longmenshan flora represents an intermediate stage in the diversification of land plants on the South China Plate, the paucity of taxa in common with both Lochkovian and later Pragian assemblages makes this unlikely.

9. Synthesis

Our investigations on the Sichuan assemblages, although their precise ages remain undecided and their sedimentological contexts unexplored, add to the burgeoning of information over the last thirty years on the diversity and disparity in Chinese early land vegetation. Prior to this, data, as recorded in Silurian and Lower Devonian rocks, were mainly derived from the palaeocontinent, Laurussia. A very different picture has emerged on the South China plate based mainly on assemblages from Yunnan subregion. The oldest records containing fragmentary rhyniophytes are in the Ngoc Vung Series in adjoining northern Viet Nam, although whether then part of the South China Plate in late Silurian times (Gonez et al. 2012) is conjectural, and on the Pridoli Yulongsi Formation from the Qujing region, Yunnan, which has yielded *Zosterophyllum qujingense* (Hao et al. 2007). A second species of *Zosterophyllum, Z. xishanense,* was recorded in the basal Lochkovian Xiaxishancun Formation in the same area (see Xue et al. 2018 for summary of controversy surrounding its age), but further diversification involving zosterophylls occurred in the overlying mid- late Lochkovian Xitun and Guijiatun Formations *(*Xue 2011). This limited diversity is in contrast to that in Laurussia where there are some zosterophylls, a few eophytes and numerous rhyniophytes (e.g. Edwards and Wellman 2001; Morris et al. 2011; Morris and Edwards 2014; Edwards et al. 2021). Extensive diversification in the Pragian of South China is particularly well illustrated by the intensively studied assemblages in the upper Pragian Posongchong Formation (Hao and Xue 2013 with limited rhyniophytes (*Hsüa*,?*Huia*) but containing numerous zosterophylls, lycophytes, barinophytes, while representatives of euphyllophytes including trimerophytes, possible sphenopsids and progymnosperms, and even a tentative pteridosperm and many taxa of uncertain affinity. In total there are almost thirty genera, the majority being endemic, but here again whether Wenshan was part of the South China Plate is open to question. Studies on the Guangxi (Cathayan) subregion are in their infancy, but the presence of a number of rhyniophytes and the endemic *Changwuia*, in the Pragian-Emsian Cangwu Formation, Guangxi, hint at a further phytoprovince (e.g. Wang et al. 2018), although the remaining genera are cosmopolitan.

The clear differences between coeval Pragian assemblages of Laurussia in terms of diversity, disparity and endemicity has been recognised in numerous phytogeographic analyses and has led to the distinction of the Chinese phytoprovince (Raymond 1987; Edwards and Berry 1991; Wnuk 1996; Wang et al. 2010; Xue et al. 2018). In addition, several authors (Hao and Gensel 1998; Hao and Wang 2000; Hao et al. 2007; Hao and Xue 2013) have emphasised similarities between Chinese and Australian Emsian taxa (upper plant assemblages: Lang and Cookson 1931; Cookson 1935). This was based on the presence of poorly preserved *Baragwanathia* sp., *Hedeia sinica*, *Zosterophyllum australianum* and *Z. ramosum,* with the probability that some of the specimens assigned to *Z. australianum* by Cookson belonged to the Chinese species (Hao and Wang 2000). Accumulated data in a current revision of the Lower Devonian of Australia in post graduate studies by Fearghus McSweeney (Mc Sweeney et al. 2020, 2021a, b, c) have strengthened links between this region and South China. Particularly important has been the combination of Victorian *Yarravia* with *Hedeia* resulting in the placing of Chinese *Hedeia* in *Yarravia* (*Hedeia*) *sinense* (McSweeney et al. 2021a). The authors also compared the Australian material with *Pauthecophyton gracile* from the Posongchong Formation (McSweeney et al. 2021b) based on similarities in aggregations of sporangia but differing in branching pattern. They concluded that such similarities combined with the two *Zosterophyllum* species (McSweeney et al. 2020) strengthened 'limited exchange' between the two regions that began possibly at least as early as the Silurian (McSweeney et al 2020, 2021a). The positioning of the Chinese and Australian localities on the northern part of Gondwana at a similar latitude had led Hao and Gensel (1998) to tentatively suggest a northeastern Gondwanan phytogeographic unit. Their proximity fits with recent palaeomagnetic data (Huang et al. 2018) although palaeogeographic reconstructions indicate some distance between the localities (Fig. 8 – locality *V*).

Is it possible to fit the assemblages of Sichuan into the above Pragian to Emsian sequences of the rest of South China? While our investigations indicate a few taxa in common and similarities in grades of organisation in South China plants, in view of the number of endemics that diversified at a slightly earlier time, we conclude that the vegetation of the Longmenshan subregion evolved in isolation from that of the southern areas, although the reasons for such isolation continue to elude us.

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Legend to plates.

Figure 1

a) *Psilophytites* sp. Developed and illustrated by Geng B-Y 1992, Plate 5, 43, 44: specimen number 8345. Scale bar = 10 mm. b) Enlargement of two spines from *a*. Scale bar = 1 mm. c) *Drepanophycus* cf. *spinaeformis* showing departing traces to ?buds/?sporangia. Arrows indicate faint striations interpreted as possible leaf traces. Note displacement of the vascular strands. Specimen number PEPB00068. Scale bar = 10 mm.

Figure 2

Drepanophycus cf. *spinaeformis.* a) Variation in leaf morphology. Specimen number PEPB00062. Scale bar = 5 mm. b) Enlargement of leaves in face and side view. Scale bar = 1 mm. c) Fragment with lateral trace entering a more darkly stained, almost circular area interpreted as a sporangium (arrow). PEPB00063. Scale bar = 5 mm. d) Dichotomous branching with division of major vascular strands. Specimen number PEPB00064. Scale bar = 5 mm. e, f) representatives of narrow stem type, named *Drepanophycus spinosus* by Geng 1992, but here named *Drepanophycus* cf. *spinaeformis*. e) Geng, plate 6, 50. Specimen number 8351. Scale bar = 5 mm. f) Note lateral branch developed from lateral buds (lower arrow) and undeveloped ?bud (lower arrow). Geng plate 6, 52. Specimen number 8352. Scale bar = 5 mm.

Figure 3

Drepanophycus cf. *spinaeformis.* a, b) Part and counterpart of narrower type, with preservation of vascular strands in a). Specimen numbers PEPB00061A, B. Scale bar = 5mm. c, d) More heavily coalified stems with possible flat apices. Specimen numbers PEPB00065, PEPB00066. Scale bars = 5 mm. e) Possible sporangium and trace magnified from *h* (arrow). Scale bar = 1 mm. f) Bases of leaves in relief. Specimen number 9269. Scale bar = 5 mm. g) Wider stems. Note displacement of strands, and faint striations and possible bud (arrow) Specimen number PEPB00067. Scale bar = 5 mm. h) Typically preserved wider stem with proximal lateral branch showing the remnants of the narrow leafy bud at base (white arrow) and probable sporangium (black arrow). Specimen number 9270. Scale bar = 5 mm.

Figure 4

Early Devonian palaeogeography of South China based on Cai and Zhang 2009 showing the localities and features discussed in the text.

Figure 5

Unidentified ?lycophyte, developed, illustrated and named *Drepanophycus spinaeformis* by Geng (1992). a) Bifurcating stem. Illustrated by Geng, plate 6, 45, where central strand more clearly seen. Specimen number 8346. Scale bar = 10 mm. b) Area of *a* magnified with longitudinally and irregularly ridged surface. White arrows indicate single strands in leaves that are perpendicular to stem. Black arrow indicates leaf inserted behind stem. Scale bar = 5 mm. c) Individual reflexed leaf with central strand (white arrow). Crescentic insertion of leaf under stem impression (black arrow). Scale bar = 5 mm.

Figure 6

Multapicifolium sinense gen. et sp. nov. a) Leafy axis with unusual preservation. Stems are compressed at right angles to the fractured surface with laminae of leaves exposed. Specimen number 9291a. Scale bar = 1. mm. b) Two of the most complete leaves in a with at least 15 distal segments indicated by arrows in *a*. Scale bar = 1 mm. c) Fragment with chaotic appearance of leaves. Specimen number PEPB00060. Scale bar = 5 mm. d) More typical preservation of leafy stem originally named *Leclercqia* and described by Geng (1992a Plate 7, 62. Specimen number - 8354). Scale bar = 5 mm. e) Close up of leaf indicated by arrow in *d*, showing laterally compressed leaf with three segments only visible. Scale bar = 1 mm.

Figure 7

Multapicifolium sinense gen. et sp. nov. Reconstruction of the leaf based on the new compression material reported here, and the SEM images of Geng (1992a). Segment morphology is taken from Fig. 6 of this paper. The morphology of the area to which the segments are attached, including the slight proximal lip, includes detail from figs 67 and 68 of Geng (1992a).

Figure 8

Palaeogeography of the Early Devonian redrawn from Torsvik and Cocks 2014. The approximate position of assemblages of Yunnan (*Y*) and Sichuan (*S*), China, and Victoria (*V*), Australia are indicated.

Table 1.

Comparisons of the dimensions of *Drepanophycus spinaeformis* and *D.* cf*. spinaeformis*.

Taxon	aerial stem width	leaf length	locality	reference
Drepanophycus spinaeformis	10-21mm	7-18mm	Canada Neotype locality	Li et al 2000
Drepanophycus cf. *spinaeformis*	<40mm	<20mm	Scotland	Raynor 1984
D. cf. *spinaeformis* type 1	1.5-(2.2)-3.0mm	0.8-(1.13)-1.7mm	Sichuan	this paper
D. cf. *spinaeformis* type 2	3.0-(3.4)-4.0mm	1.6-(2.6)-3.1mm	Sichuan	this paper

Table 2.

Summary of taxonomic revision of the Sichuan Lower Devonian plant fossil assemblages.

Geng 1992 (a+b)	Revisions	Affinity	Comments on endemicity
Eogaspesiea gracilis	Not studied	?	identification unreliable
	Jiangyounia gengi 2018a	R	endemic
	Polycladophyton gracilis 2018a	R	endemic
Zosterophyllum myretonianum	*Z. ovatum* 2018b	Z	Species confined to Sichuan
Z. yunnanicum	Not studied	Z	Species also in Qujing,Guizhou, cf. in Guangxi
Z. sichuanensis	*Ornicephalum sichuanense* 2018b	Z	endemic
	Guangnania minor 2016	Z	genus also in Wenshan & Qujing
Hicklingia cf. *edwardii*	*Bauyinia sichuanensis* 2018a	Z	endemic
-	*Sichuania uskielloides* 2018a	Z	endemic
-	*Adoketophyton pingyipuensis* 2018b	B	genus also in Wenshan
Amplectosporangium jiangyouense	*A. jiangyouense* Geng 1992b	?	endemic
Oricilla unilateralis	*Amplectosporangium (Oricilla) unilaterale* 2018b	?	endemic
-	*A. unilaterale forma minor* 2018b	?	endemic
Zosterophyllum longa	*Yanmenia (Zosterophyllum) longa* (2016)	?	endemic
Drepanophycus spinaeformis	*Drepanophycus* cf.*spinaeformis* (this paper)	L	?cosmopolitan
D. spinosus	*Drepanophycus* cf.*spinaeformis* (this paper)	L	?cosmopolitan
D. sp.	(New genus)	L	Further studies needed
Leclercqia complexa	*Multapicifolium sinense* (this paper)	L	endemic

R = Rhyniopsida, Z = Zosterophyllopsida, L = Lycopsida, B = Barinophyta

Sources for revisions: Edwards et al. 2016, Edwards and Li 2018a, Edwards and Li 2018b, Geng 1992b.

Table 3.

Diversity data from South China.

Taxa	Wenshan	Qujing	Guangxi	Guizhou	Longmenshan
Rhyniopsida					
Jiangyounia gengi	n	n	n	n	*
Polycladophyton gracilis	n	n	n	n	*
Zosterophyllopsida					
Discalis longistipa	*	n	n	n	n
Bauyinia sichuanensis	n	n	n	n	*
Distichophyton sp.	✓	n	n	n	n
Guangnania cuneata	X	X	n	n	n
Guangnania minor	n	n	n	n	X
Gumuia zyzzata	*	n	n	n	n
Oricilla sp.	✓	n	n	n	n
Ornicephalum sichuanense	n	n	n	n	*
Ramoferis amalia	*	n	n	n	n
Sichuania uskielloides	n	n	n	n	*
Wenshania zhichangensis	*	n	n	n	n
Yunia dichotoma	X	n	n	n	n
Yunia guangnania	X	n	n	n	n
Zosterophyllum australianum	✓	✓	n	n	n
Zosterophyllum bifurcatum	n	✓⊗	n	n	n
Zosterophyllum dushanense	n	✓⊗	n	✓⊗	n
Zosterophyllum minifertillum	✓⊗	n	n	n	n
Zosterophyllum ovatum	n	n	n	n	✓⊗
Zosterophyllum ramosum	✓⊗	n	n	n	n
Zosterophyllum sinense	n	n	✓⊗	n	n
Zosterophyllum spathulum	n	✓⊗	n	n	n
Zosterophyllum tenerum	✓⊗	n	n	n	n
Zosterophyllum yunnanicum	n	✓ ⊗	cf	✓⊗	✓⊗
?Zosterophyllopsida					
Demersatheca contigua	*	*	n	*	n
Lycopsida					

Baragwanathia sp.	✓	n	n	n	n
Drepanophycus qujingensis	n	✓ ⊗	n	n	n
Drepanophycus cf. *spinaeformis*	n	✓	✓	?	✓
Halleophyton zhichangense	*	n	n	n	n
Huia gracilis	n	X	n	n	n
Huia recurvata	X	n	n	n	n
Multapicifolium sinense	n	n	n	n	*
Zhenglia radiata	*	n	n	n	n
?Lycopsida					
Hicklingia sp.	✓	n	n	n	n
Hueberia zhichangensis	*	n	n	n	n
Yanmenia longa	n	n	n	n	*
Barinophytales					
Adoketophyton parvulum	X	n	n	n	n
Adoketophyton pingyipuensis	n	n	n	n	X
Adoketophyton subverticillatum	X	n	n	n	n
?Barinophytales					
Dibrachophyton acrovatum	*	n	n	n	n
Bracteophyton variatum	n	*	n	n	n
Trimerophytopsida					
Psilophyton primitivum	✓⊗	n	n	n	n
Psilophyton princeps	n	n	n	?	n
Pauthecophyton gracile	X	n	n	n	n
Pauthecophyton hezhangensis	n	n	n	X	n
Basal Sphenopsida					
Estinnophyton yunnanense	✓⊗	n	n	n	n
?Basal Sphenopsida					
Cervicornus wenshanensis	*	n	n	n	n
Basal Progymnospermopsida?					
Polythecophyton demissum	*	n	n	n	n

Basal Lignopterid Pteridospermatophyta?					
Celatheca beckii	*	n	n	n	n
Incertae sedis					
Amplectosporangium jiangyouense	n	n	n	n	X
Amplectosporangium unilaterale	n	n	n	n	X
Catenalis digitata	*	n	n	n	n
Changwuia schweitzeri	n	n	*	*	n
Eophyllophyton bellum	*	n	n	n	n
Yarravia (*Hedeia*) *sinica*	✓⊗	✓⊗	n	n	n
Hsüa robusta	n	X	n	n	n
Hsüa deflexa	n	X	n	n	n
Stachyophyton yunnanense	*	n	n	n	n
Number of Species	33	14	4	5 (+2?)	14
Number of Genera	29	8	3	4 (+2?)	12
Number (percentage) of local endemic genera	15 (52%)	2 (25%)	0 (0%)	0 (0%)	8 (67%)
Number (percentage) of South China endemic genera	21 (72%)	5 (63%)	1 (33%)	3 (75%)	10 (83%)

- * = South China endemic genus
- X=species of South China endemic genus
- √/tick=non-South China genus
- ⊗= endemic species of non-South China genus
- n=not present

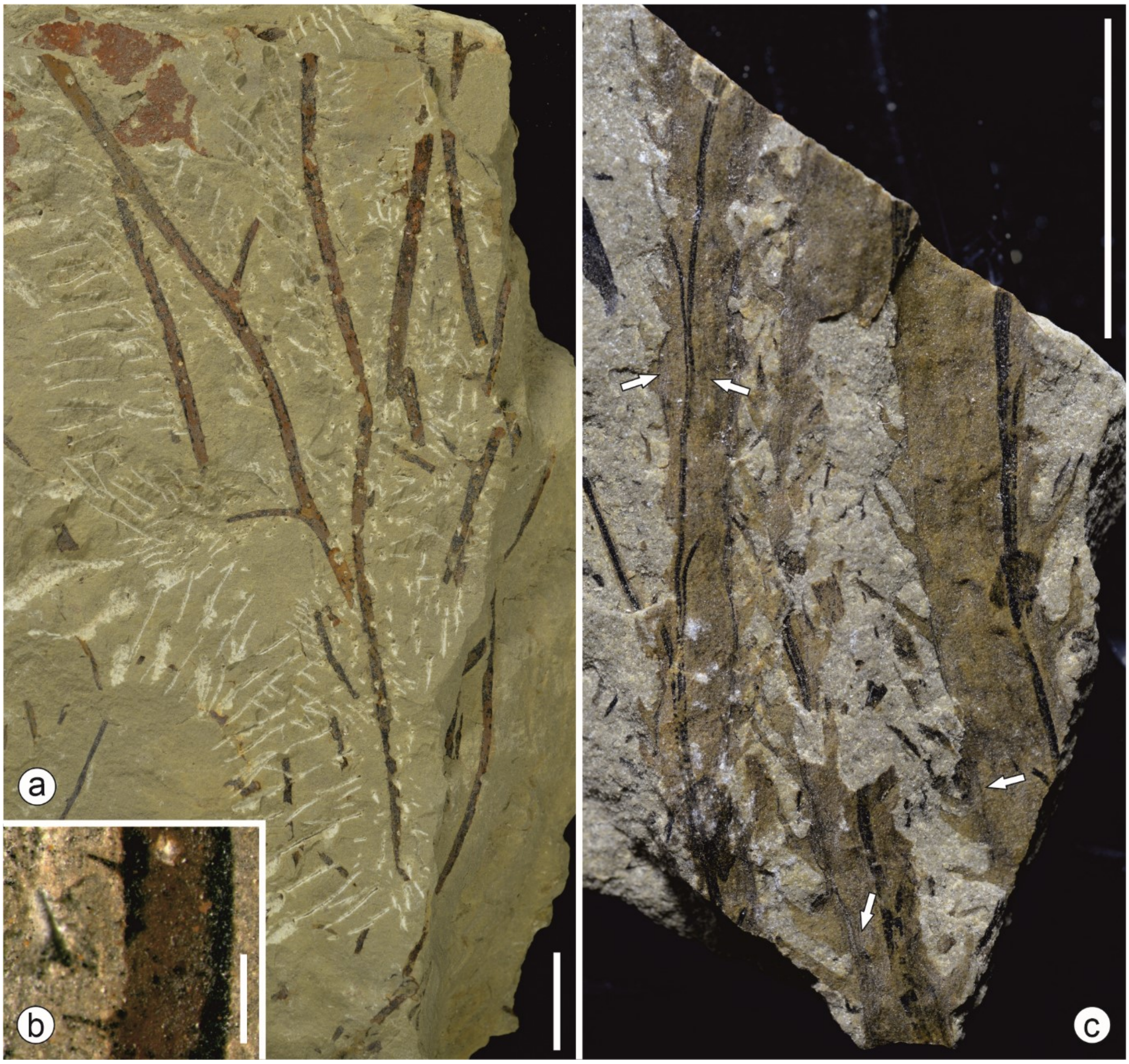
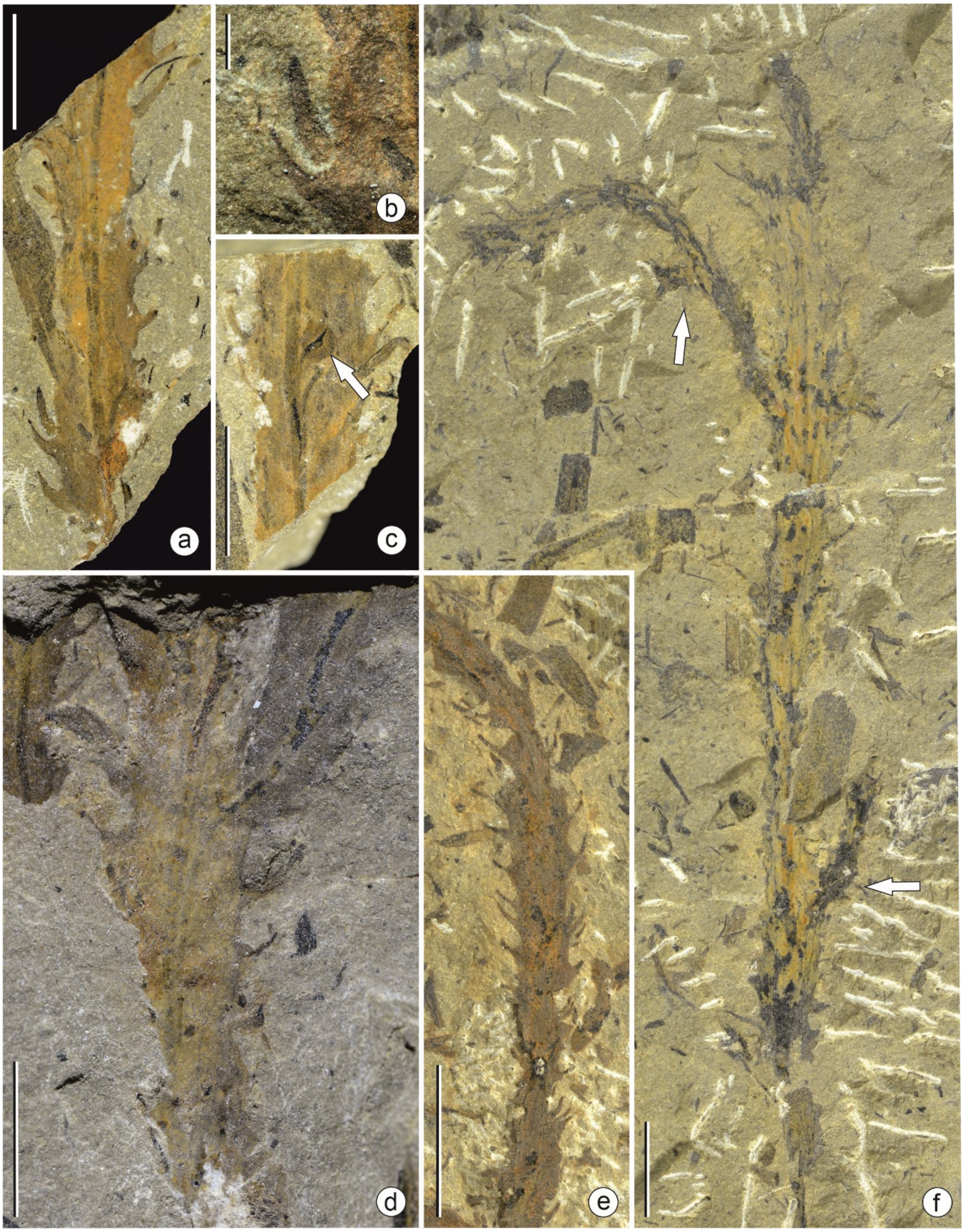


Figure 1



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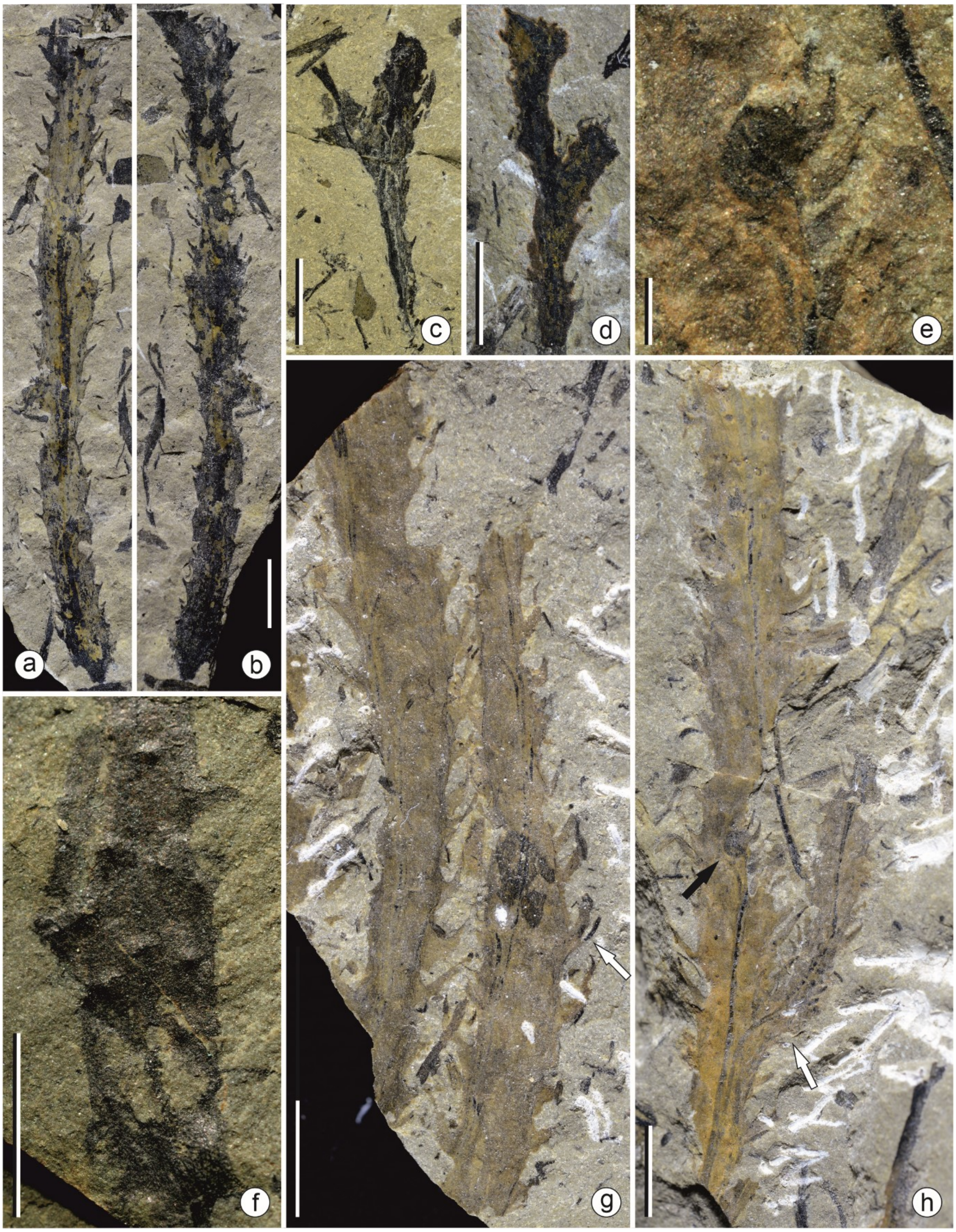
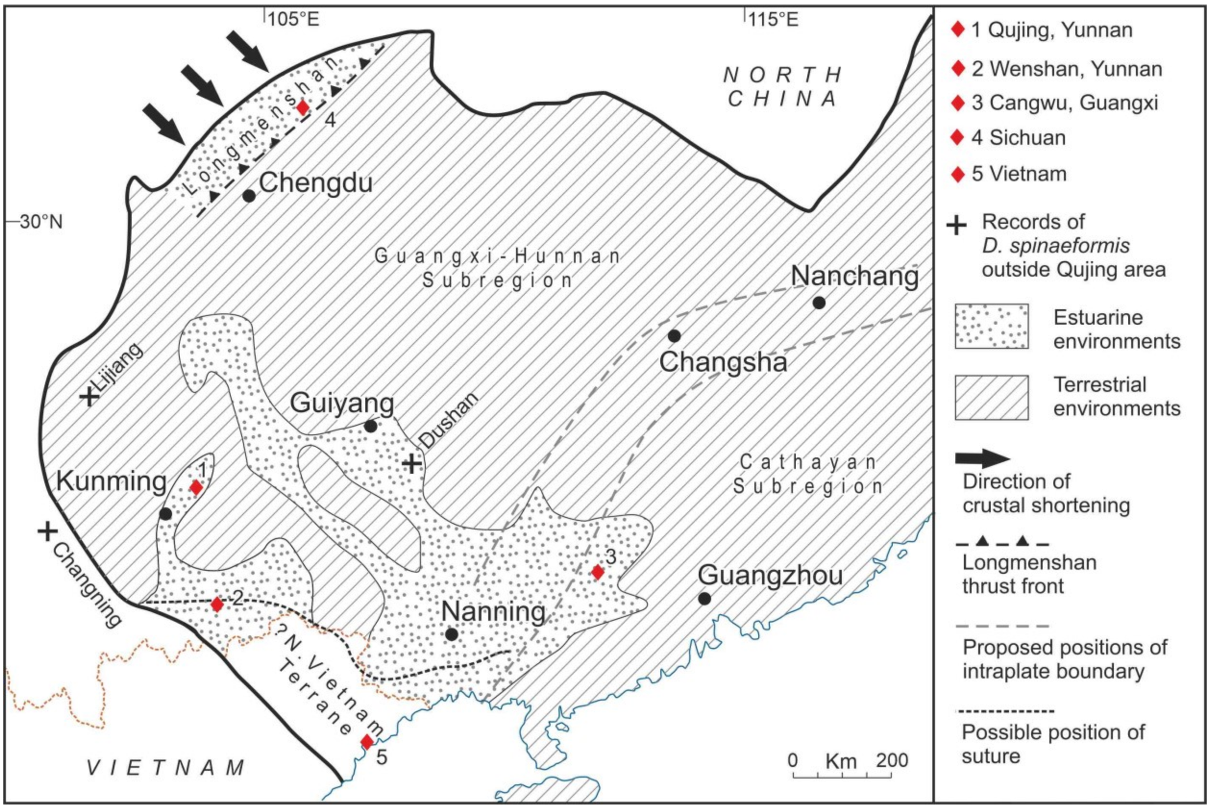


Figure 3


105°E
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NORTH CHINA
Longmenshan
4
Chengdu
Guangxi-Hunnan Subregion
Nanchang
Changsha
Lijiang
Guiyang
Dushan
Kunming
1
Cathayan Subregion
Changning
3
Guangzhou
2
Nanning
?N. Vietnam Terrane
5
VIETNAM
0 Km 200
1 Qujing, Yunnan
2 Wenshan, Yunnan
3 Cangwu, Guangxi
4 Sichuan
5 Vietnam
Records of *D. spinaeformis* outside Qujing area
Estuarine environments
Terrestrial environments
Direction of crustal shortening
Longmenshan thrust front
Proposed positions of intraplate boundary
Possible position of suture

Figure 4

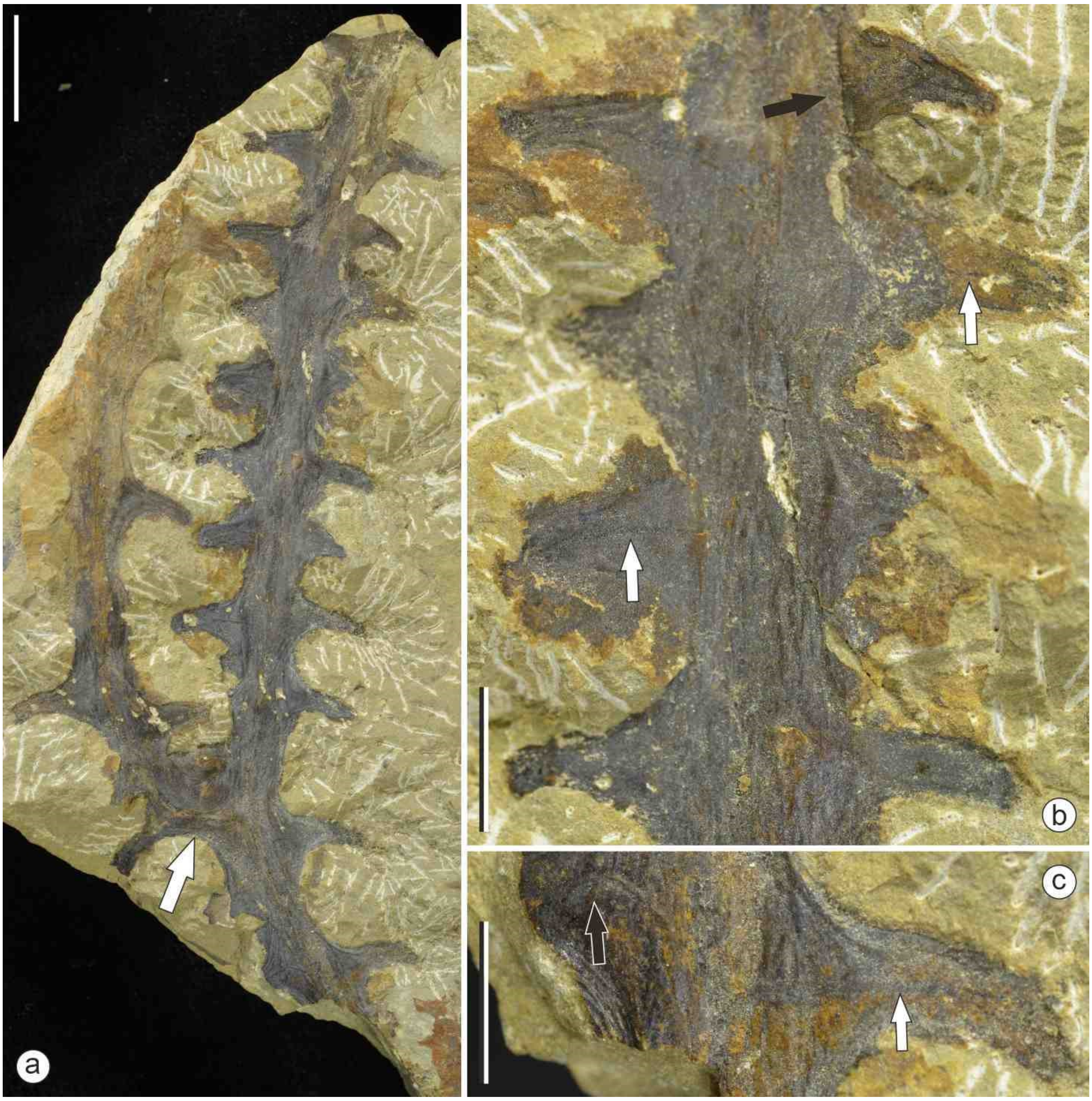

Figure 5

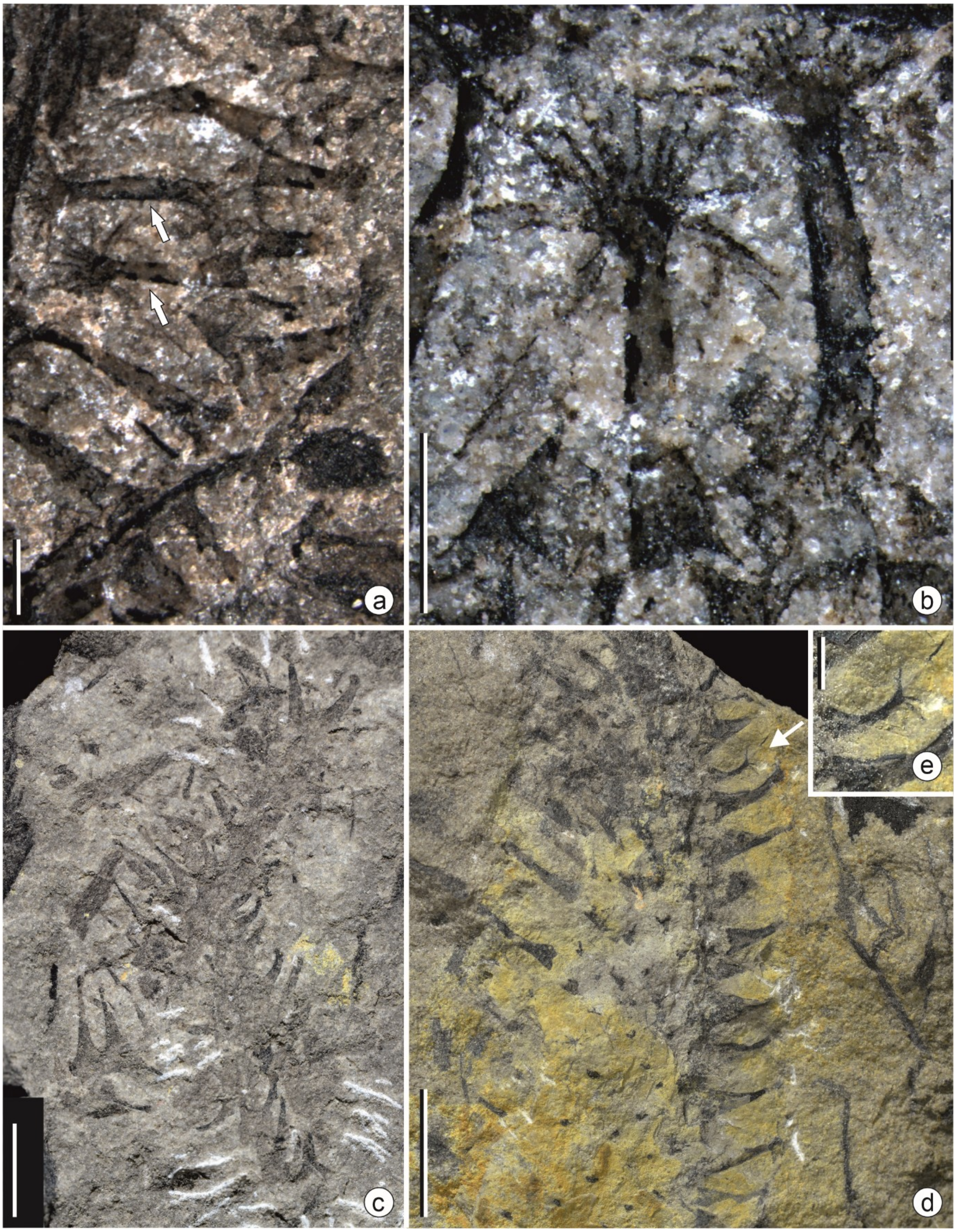

Figure 6

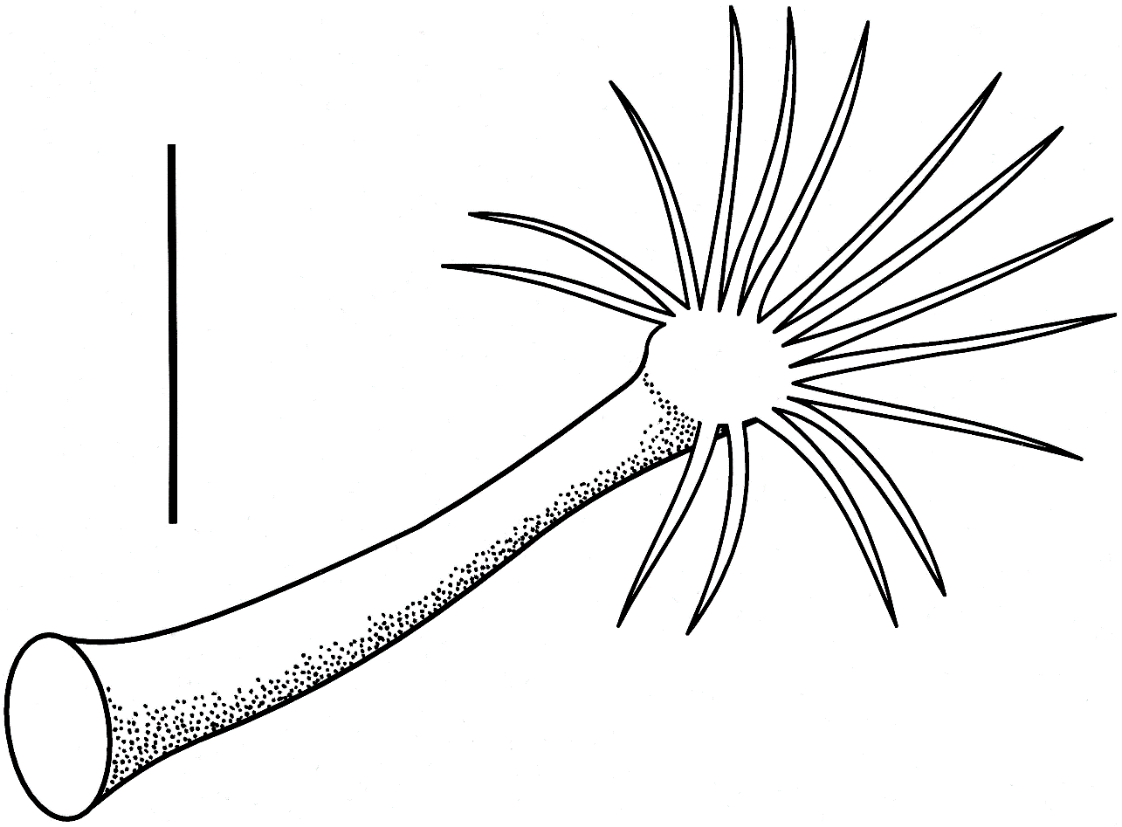

Figure 7

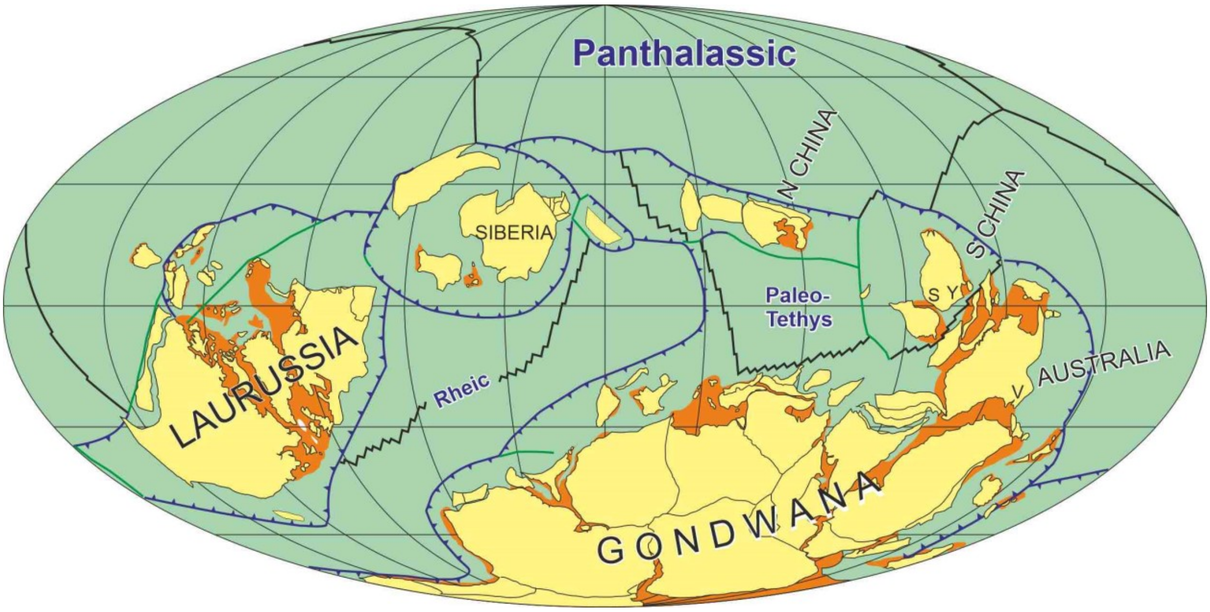
Panthalassic
N CHINA
SIBERIA
S CHINA
S Y
Paleo-Tethys
LAURUSSIA
Rheic
V
AUSTRALIA
GONDWANA

Figure 8