Diversity in affinities of plants with lateral sporangia from the Lower Devonian of Sichuan Province, China

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Abstract

Five plant species, all with lateral sporangia aggregated into strobili terminating smooth stems, have been circumscribed from the Lower Devonian Pingyipu Group exposed in Jiangyou County, Sichuan, China. Four have involved reinvestigation of fossils described more than twenty years ago plus, in some instances, observations on more recently collected fossils, while the fifth, *Adoketophyton pingyipuensis* sp. nov., unusual in that the strobilus contains bracts, is based on new material. The fossils are preserved as coalified compressions and impressions and lack anatomy. *Zosterophyllum ovatum* was originally called *Z. myretonianum*, but mainly differs from the type species in sporangial shape. The plant first named *Z. sichuanensis* has been placed in a new genus *Ornicephalum*, because it possesses bivalved sporangia with markedly unequal valves. Two species of *Amplectosporangium*, whose terminal fertile complexes are unique because they comprise collections of dichotomously branching axes bearing rows of sessile or almost sessile sporangia, are distinguished by the amount of branching in the fertile complex and on sporangial shape. That with simpler branching was originally placed in the North American genus *Oricilla*. The classification of the zosterophylls, relationships within the lycophytes and, in this study, particularly the affinities of *Adoketophyton,* here considered a barinophyte, require revision. Considering geographical relations, at species level all taxa are restricted to the locality. At generic level, *Zosterophyllum* is cosmopolitan, *Adoketophyton* is also recorded in Yunnan, while *Amplectosporangium* and *Ornicephalum* are restricted to Sichuan, providing further evidence for the preponderance of endemicity in Chinese Lower Devonian vegetation while reinforcing differences between the assemblages in the two Chinese provinces. The reasons for this remain conjectural.

Keywords

Endemics; Lochkovian-Pragian; Lower Devonian; plant megafossils; Sichuan tracheophytes.

1. Introduction

This is the third paper in a series recording descriptions of new taxa and reinvestigation of those originally described by Geng (1992a, b) from the Lower Devonian Pingyipu Group, Sichuan. We earlier had emphasised the need for such studies based on new and original collections in the light of more recent discoveries in the approximately coeval Lower Devonian plants from Yunnan (e.g. Posongchong Formation; Hao and Xue, 2013), which have demonstrated a high degree of endemicity. Our first two papers have indicated a similar situation in Sichuan with all but one of the new genera, viz. *Baoyinia, Yanmenia, Jiangyounia*, *Sichuania* and

Polycladophyton, not found elsewhere. The exception is *Guangnania* (Wang and Hao, 2002) which is also recorded in Yunnan (Edwards et al., 2016; Edwards and Li, submitted). Here we report on five further taxa from the Pingyipu Group, which are united in their possession of lateral sporangia, but these are aggregated into a variety of terminal complexes such that their affinities mostly extend outside the traditional concept of the Zosterophyllophytina *sensu* Banks (1968). This demonstrates the need for a fundamental reassessment, as has begun with more recent cladistical analyses (e.g. Kenrick and Crane, 1997; Hao and Xue, 2013).

2. Locality, stratigraphy and age

Earlier papers (Edwards et al., 2016; Edwards and Li, *in press*) have provided information on the Lower Devonian rocks of the Tangwanzhai Syncline, including the exposure in the lower part of the Pingyipu Group exposed near Yanmenba, Jiangyou County, Sichuan, which has yielded the fossils described here. The section extends from the Lochkovian to the upper Pragian and the plants all come from the base of the sequence (Horizon 1 in Edwards et al., 2016). There are no direct independent data on the age of the deposit, but a number of lines of evidence summarised in Edwards et al. (2016) point to a Lochkovian age although there remains the possibility of a Pragian one. Our discovery of eurypterid fragments, the first animals found at the locality, have some relevance as environmental indicators, because they lived in marginal marine to brackish / fresh water habitats, but their stratigraphic range is too wide to be useful in dating.

3. Material and methodology

The fossils are preserved as compressions, comprising sheets or grains of coalified material, or impressions, either iron-stained or slightly darker than the matrix, which is a buff-coloured, coarse siltstone. The specimens described here are occasionally found isolated on slabs devoid of other fossils (e.g. *Adoketophyton*), but the majority are intermingled with sometimes branched plant fragments. These are usually smooth, very occasionally 'leafy,' and of varying diameter and length, showing no particular orientation. Further exceptions include the specimens of *Zosterophyllum* and *Amplectosporangium* (*Oricilla*) where fertile stems occur in parallel with fertile zones at the same level, suggestive of preservation of more complete plants and indicative of limited transport, but with some current alignment. Some specimens show variation in appearance across a single slab. Thus, for example, *A. jianyouense* may be preserved as a heavily coalified, black, glossy compression (e.g. Plate IV, 8), but in an area close-by the same taxon appears as an impression, slightly darker that the siltstone (e.g. Plate IV, 10). Similar differences are apparent in the surrounding debris. This results from oxidation sometime post fossilisation, when seepage along bedding planes occurred along faults and bedding plane weaknesses. Finally a number of specimens have deteriorated such that only streaks of coal remain.

Specimens were examined under dissecting microscopes in Cardiff and Beijing, followed by photography, in Cardiff using polarised light. In Cardiff, higher resolution was achieved with a LEICA MZ16 stereo microscope using Leica Application Suite (LAS) software to capture images. A similar system was used in Beijing. Fragments of coalified material were treated with Schultz solution, but yielded neither anatomical information nor spores.

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

4. Descriptions of taxa

4.1. *Zosterophyllum ovatum* (*Z. myretonianum* Geng, 1992a) sp. nov.; Plate I.

4.1.1. *Description*

Geng (1992a) illustrated three specimens (8321) pl. 1, figs. 1, 5, 6; 8321 counterpart , pl. 1,fig. 2; 8322, pl. 1, figs. 3, 4) which he identified as *Zosterophyllum myretonianum* Penhallow based on long unbranched parallel-sided axes terminated by strobili composed of spirally arranged, lateral, bivalved sporangia borne on short stalks. Our reinvestigation of his specimens confirmed the gross morphology and his choice of genus, but differ in interpretation of strobilar and some sporangial features. His preparations with spores (pl. 1, figs. 7, 8) and tracheids (pl. 1, fig. 9) were not available. Two of the original specimens are illustrated here (Plate I, 1, 2).

Sporangia in face view are oval in outline (Plate I, 1), 3.6-5.2 mm wide and 2.5-3.8 mm high, and borne of parallel-sided stalks, 0.3-1.4 mm wide, which show little or no change in diameter at the junction (Plate I, 2, 3). Stalk length is difficult to measure, because there is little superficial change in appearance at the sporangial junction. However, rare examples, with imprints of cells on the underlying rock in the absence of the coalified material, show an abrupt horizontal change from more or less isodiametric outlines (Plate I, 7) in the sporangial region to elongate on the stalk. The free margin of the sporangium is marked by a narrow continuous border, 0.1-0.2 mm wide (Plate I, 3, 4, 7) which remains adhered to the rock as a strip of coalified material or impression when the rest of the sporangium has disappeared, but is not characterised by a marked thickening. Indeed, on some more completely preserved sporangia, a border cannot be distinguished, although its position may be marked by a groove or ridge. In a few examples, a 'double border' is interpreted as indicating the presence of two valves Plate I, 7 (arrow). Where sporangia are attached to the sides of the axes, they are usually not folded and laterally compressed such that half an abaxial valve is preserved (but see Plate I, 6), but are narrower with greater thickness of coal (Plate I, 5). In such compressions, a line sometimes marks the position of the junction between two valves or the adaxial margin is represented by a ridge.

In profile the stalks are usually straight (Plate I, 5) and attached at varying angles to the strobilar axis. In most fragments of strobili, they are widely separated and up to four per fragment, but Plate I, 4 shows a more crowded example that is interpreted as a possible apex of helically arranged, mostly folded sporangia. Geng (1992a) illustrated similar arrangements in his pl. 1, fig. 1, where the same specimen shows a possible bifurcation in the region where sporangia are more widely spaced. Very limited evidence, based on superficial mounds, suggests that the sporangia were inserted irregularly on all sides of the strobilar axes, although the spacing on some of the fragments points to a rowed arrangement. The subtending vegetative axes are at least 80 mm long. There is no evidence of branching.

4.1.2. *Comparisons with Zosterophyllum myretonianum*

In the Scottish type species, there are significant differences in sporangial features. Lateral sporangia are borne on short curved stalks and the junction may be convex. This, combined with slight basal lobing of the valves, produces a reniform shape. In addition, where borders are preserved, they are wider. Edwards (1975) showed intraspecific variation in sporangial spacing on the strobilus ranging from closely spaced, sometimes confined to the apex, to more proximally separated examples. Thus on sporangial morphology and insertion we dispute the conspecificity of the Sichuan fossils with *Z. myretonianum* but agree that they belong to that genus.

4.1.3. *Broader comparisons*

A comprehensive synopsis of more than 16 species of *Zosterophyllum,* including Chinese examples with helically inserted sporangia, was provided by Hao and Xue (2013). They did not include a further four with one or two-rowed arrangement (usually placed in *Platyzosterophyllum*), because this organisation is not found in China. In the former type, they distinguished those with close (overlapping) sporangia from widely spaced loosely arranged examples. The latter, which are closer to the Sichuan material, included Chinese species, *Z. sinense* Li and Cai 1977, *Z. shengfengense* Hao et al. 2010 and *Z. tenerum* Hao and Xue 2013, and, from the Belgian Emsian, *Z. deciduum* Gerrienne 1988.

Zosterophyllum sinense was one of the numerous species of *Zosterophyllum* described by Li and Cai (1977), many of which require re-examination. *Zosterophyllum sinense* is one of the better known, with sporangia of similar dimensions to Sichuan examples, but lower width to height ratio with a proximal taper into the stalks. In lateral view, they show a similar orientation being borne on very short stalks. Poor reproduction of images prevents further detailed comparison, but the relatively compact strobili further allow distinction from the Sichuan material. A very small fragment named *Zosterophyllum* B (Li and Cai 1977, pl. V 12, 12a) requires further investigation because it has similarly-shaped sporangia in face view, but with broad borders. Considering the remaining Chinese species with lax spikes, *Z. tenerum* differs in sporangial shape, which was described as pear shaped and thus closer in full valve view to the *Sichuania* forms recently described in the Sichuan assemblage (Edwards and Li, *in press*). *Zosterophyllum tenerum* sporangia have a broad marginal feature with dehiscence at the base of a groove. Unfortunately detailed illustration of sporangial details for Lochkovian *Z. shengfengense* from Yunnan are not included in a paper that concentrated on root/shoot relationships in the most completely known *Zosterophyllum* plant (Hao at al., 2010). Sporangia, broadly similar in face view to the Sichuan material, were described as round and reniform, scattered in lax spikes and borne on short ?straight stalks inserted at acute angles. Dehiscence was reported as into two valves, but no information was provided on marginal features, although an illustrated example shows a conspicuous border (Hao et al., 2010, fig. 2c) and possible tapering of the sporangium into the stalk. Thus on sporangial characters, the Sichuan material stands apart, but more information is needed on the Lochkovian species from Yunnan.

There remains *Z. deciduum* from the Belgian Emsian (Gerrienne, 1988), a zosterophyll with unique growth habit comprising branching horizontal axes and short, almost entirely fertile, upright ones revealing abscission of sporangia. The latter, oval in face view (0.7-2.35 mm wide, average = 1.47 mm; 0.7-1.8 mm high, average = 1.23 mm) are borne on straight or slightly curved stalks (0.3-1.25 mm wide; 0.7-1.0 mm high) and comprise two valves with thick-walled borders. In this and in the position of the strobili, the Belgian Laurussian species differs from the Sichuan specimens and provides further support for the reception of a new species.

4.1.4. *Systematic palaeobotany*

Subdivision: Lycophytina.

Basal lycophytes *sensu* Kenrick and Crane 1997 or Zosterophyllaceae Hao and Xue 2013.

Genus: Zosterophyllum Penhallow.

Type species: *Z. myretonianum*.

Species: ***Zosterophyllum ovatum* Edwards and Li sp. nov.**

Diagnosis: Plant with ?unbranched stems at least 80mm long and c.1.5 mm wide terminating in lax strobili. Sporangia with two equal valves, oval in face view (3.6-5.2 mm wide; 2.5-3.8 mm high), sporangial border 0.1-0.2 mm wide. Sporangia borne on short, straight axes (0.3-1.4 mm wide); junction between sporangium and stalk horizontal. Lax strobili lacking regular insertion of sporangia.

Etymology: From the Latin *ovatus* = oval, referring to the valve outline in face view.

Holotype: 8321, figured by Geng 1992a, pl. 1, figs 1 & 2.

Locality: Yanmenba section, Jiangyou district, Sichuan 32°13.87'N, 105°10.98E.

Stratigraphy and age: Horizon 1 in the Pingyipu Group, Lochkovian/Early Pragian, Lower Devonian.

4.2. *Ornicephalum (Zosterophyllum) sichuanense* gen. et sp. nov.*;* Plate II, 1-10.

4.2.1. *Description*

The original description was based on three specimens named *Z. sichuanense* (Geng 1992a, pl. 2, figs. 10-14). Two are in part and counterpart and show loose aggregations of sporangia thought to represent the bases of strobili which terminate long, parallel-sided, smooth stems (1.5-1.8 mm wide). The longer specimen (8324a) attains c. 60mm (Plate II, 9). This specimen also has the longest strobilar fragment (1.9mm long) containing six sporangia. Complete sporangia in all specimens are preserved in side view and are borne on narrow parallel-sided stalks that are curved adaxially with only slight increase in diameter at either end. The abaxial margin of the stalk is continuous with that of the abaxial valve of the sporangium, while an immediately adjacent longitudinal raised band (8323a, b) suggests that the stalk itself was fused to the sporangium in this region (Plate II, 2, 4). All specimens superficially show a two-rowed sporangial arrangement, but there is some evidence for three dimensional organisation based on slight variations in level of attachment towards the edges of the strobilar axis, the presence of a faint scar and associated imprint of a possible stalk on an axial surface (Plate II, 4), and the anomalous, imperfectly preserved, structure terminating a narrow straight stalk that emanates from the upper surface of the strobilar axis at its base (Plate II, 9). The laterally compressed sporangia are transversely extended adaxially (Plate II, 2-4, 6-9), the marked asymmetry due to the abaxial attachment of the stalk. The entire distal margin shows convex curvature but the proximal is more or less straight and inclined or curved towards the stalk (Plate II, 2, 4, 8). The junction at change of shape may be rounded or almost pointed Plate II, 4, 8). Some sporangia on all strobili bear a line, ridge or groove extending from the adaxial surface close to the change in curvature and running almost parallel to the proximal margin to just over half of sporangial diameter (Plate II, 2-4, 6-7). The whole sporangium thus resembles a bird's head with short beak. The linear feature is interpreted as involved in separating the larger distal (abaxial) valve of the sporangium from a smaller proximal (adaxial) one. It may extend to the inner limits of the fused stalk (Plate II, 2). In one sporangium only, a circular depression is present towards the centre of sporangium (Plate II, 8). The mark in Plate II, 6, 7 was produced by a needle. Apart from rare impressions of cells on the abaxial valve (Plate II, 5), no anatomical data have been preserved on the iron stained impressions.

The lack of distinction between the stalk and sporangium and the asymmetry of the latter hamper accurate measurement of sporangial dimensions. These are summarised in Table 1.

4.2.2. *Discussion on affinities*

Geng (1992a) compared the lateral sporangia with those of *Zosterophyllum myretonianum* and *Z. llanoveranum,* and on shape and sporangial distribution in the strobili concluded that they should be placed in the genus *Zosterophyllum*, but as a new species, *Z. sichuanense*. We have failed to find reniform to transversely elliptical sporangia formed of two valves of equal size in any of his specimens, and thus see no affinity with strobilate zosterophylls nor with taxa where sporangia are more dispersed, e.g. *Gosslingia*. Our interpretation of the sporangia as formed of two very unequal valves allows comparison with two Emsian North American taxa, *Sawdonia ornata* and *Crenaticaulis verruculosus*, and Belgian *Ensivalia deblondii* (Gerrienne, 1996) as well as some fragmentary examples from China. The first two have lax strobili, but their stems are spiny (*Sawdonia*) or with one or two rows of teeth (*Crenaticaulis*). A detailed recent analysis of material from the type locality of *Sawdonia* (Gensel and Berry, 2016) indicates marked asymmetery of the valves with the "larger rounded outer abaxial valve in which the stalk merges imperceptibly into the back of the valve", while in *Crenaticaulis*, Banks and Davis (1969) reported that the "pedicel recurves upwards towards the stem widens slightly distally and merges smoothly with the abaxial side of the sporangium" and considered that dehiscence began just above the junction of stalk and sporangium and arched over its adaxial surface and ended in a similar position on the other side, thus producing a larger abaxial and small adaxial "portions". Neither taxon possessed a thickening associated with the dehiscence line, and in *Sawdonia* it was reported that "each valve has a narrow flat rim not readily visible unless the sporangium is open" – an observation that might account for the apparent absence of a dehiscence line on some of the Sichuan sporangia preserved as impressions. Considering the Chinese representatives, Xue (2009) had briefly described a fertile fragment named *Xitunia spinitheca*.from the Lochkovian Xitun Formation in the Qujing area comprising four vertical rows of laterally compressed sporangia in which a large abaxial valve bore long spiny appendages over the distal margin.

All the above taxa bear enations, but a naked form with possible asymmetric valves is present in a single Chinese Lochkovian specimen from Yunnan (Xue, 2012). The strobilus here consisted of helically inserted reflexed sporangia borne on adaxially curved long stalks. In lateral view sporangial outline is oval and shows a dehiscence line “arching from one side of the sporangium over the adaxial face to the opposite side dividing the sporangium into two equal valves (p. 339)”. The dotted lines in the line drawing (Xue, 2012, fig. 5c) representing the dehiscence lines are in a similar position to those in the Sichuan specimens. Xue compared the plant with *Huia recurvata* and *H. gracilis* (Wang and Hao, 2001), but, noting differences in sporangial dehiscence, named it aff. *Huia* sp. Further information is also required to relate it to the Sichuan material, but it is considered unlikely that the latter is close to *Huia*.

Both North American taxa were preserved in compressions with distinctive cuticular fractures and permineralisations which revealed large, xylem strands elliptical in transverse section and characteristic of the Zosterophyllophytina *sensu* Banks. Absence of this latter information as well as stem enations persuade us that the Chinese specimens should be placed in a new genus, named *Ornicephalum*, but its relationship within the Zosterophyllopsida *sensu* Hao and Xue (2013) requires more data. Based on sporangial organisation, it would be assigned to the

Zosterophyllales, but in sporangial construction it shows greater similarities with the Gosslingiales.

4.2.3. *Systematic palaeobotany*

Subdivision: Lycophytina

Basal lycophytes *sensu* Kenrick and Crane 1997 or Zosterophyllaceae Hao and Xue 2013.

Genus: ***Ornicephalum* Edwards and Li gen. nov.**

Diagnosis: plant with smooth stems terminating in lax strobili composed of bivalved sporangia inserted helically and supported by long distally curved stalks. Sporangia consist of two unequal valves, the smaller being adaxial and separated from the larger abaxial valve by an almost transverse dehiscence line. Stalk merges with the outer surface of the abaxial valve such that no junction is visible.

Etymology: Latinized from the Greek: ornis (m) = bird and kephalis (f. dim) = head referring to the outline of the sporangium.

Type species: ***Ornicephalum sichuanense* (Geng) Edwards and Li comb. nov.**

Basionym: *Zosterophyllum sichuanensis* Geng 1992a. Studies on Early Devonian flora of Sichuan. Acta Phytotaxonomica Sinica 30, 197-211, pl. 2, figs. 10-14.

Species diagnosis: As for genus. Plant at least 60mm tall, stem width 0.8-1.7mm. Strobilar length greater than 15mm. Sporangia 1.5-2.7mm high; 1.6-2.8mm maximum width. Sporangial stalks 0.6-1.1 wide at mid-point, 1.5-4.2mm long.

Etymology: From the Chinese Province of Sichuan.

Holotype: 8324.

Locality: Yanmenba section, Jiangyou district of Sichuan. 32°13.87'N, 105°10.98'E.

Stratigraphy and age: Horizon 1 in the Pingyipu Group, Lochkovian/early Pragian, Lower Devonian.

4.3. *Adoketophyton pingyipuensis* sp. nov.; Plates II, 11-14; III, 1-2; IV, 1-5.

4.3.1. *Description*

The description is based on two specimens both preserved in part and counterpart collected from Horizon 1. The more informative, specimen 8534a & b, is three dimensionally preserved with some coalified material remaining on more darkly coloured impressions (Plate III, 1, 2). The second, showing poorer preservation, is more compressed and an iron-stained impression in which fertile structures are less easily distinguished (Plate IV, 1-5). Both specimens comprise just the strobilus composed of a number of lateral sporangial complexes (c.15). Each complex has two parts, an abaxial bract bearing an adaxial sporangium, and is attached to the strobilar axis by a short, curved stalk. In the type specimen, the strobilus, incomplete both proximally and distally, is three cm long and contains nine complexes preserved in their entirety or broken, with at least six more indicated by attachment sites of the stalks (Plate III). The complexes were not inserted in vertical ranks, but were borne on all sides of the axis: whether or not a regular helical arrangement was present could not be determined. The stalks are inserted at an angle and adaxially curved so that the complex is upright and only slightly, if at all, inclined away from the strobilar axis. The height of a single complex from attachment to the distal tip of the bract is 4.0-6.0 mm (the largest at strobilar base) (n=7) and the majority are 4.0 mm. Stalks are parallel-sided except at their bases, where they increase in diameter and are slightly decurrent, and where they expand imperceptibly into the base of the bract complex. Stalk length is thus impossible to measure with confidence (c.1.0-2.0 mm, x=1.4 mm, n=5). Most of the complexes on the holotype are visible only in lateral view. That illustrated in Plate II, 14 is an exception. The most complete face view of the bract is exposed in the second specimen where it has a fan-shaped outline, with slightly convex extremity, rounded margins and straight sides (Plate IV, 3, 4). In side view, where the bract is interpreted as laterally compressed, folded or fractured, the abaxial margin is continuous with that of the stalk, is straight or gently concave and then flexed abaxially (Plate II, 12,13; III, 1, 2). Distally, the bract may taper to a rounded apex or may be less attenuated with flattened extremity (Plate II, 13). In one uncovered specimen, it is partially curved around the sporangium concealing the latter (Plate II, 12, 13). The extent to which the bract enclosed the sporangium in life is unknown, but it almost encircles/covers it in laterally compressed examples. In some exposed examples, a sporangium is attached without obvious stalk to the base of the bract (Plate II, 11) close to where the latter begins to expand. Although it often cannot be distinguished from the bract itself, it is considered unlikely that sporangia were fused with it (e.g. Plate II, 12, 13). Thus exposed well-defined sporangia are rare: they are ovate and vertically extended, either upright or slightly inclined towards the strobilar axis. A vertical line is hinted at on one sporangium (Plate II, 11). The most complete sporangia are 0.7-0.9 mm wide, and length varies between 0.9 and 1.2 mm. In the most informative example of the complex, the overall length is 5.0 mm, and 1.5-2.0 mm wide, the sporangium is attached c. 1.0 mm above the junction of stalk and bract (i.e. a quarter way up the complex) and covers about two thirds of bract lamina. The bract itself extends a millimetre above the sporangium. Spores have not been isolated.

4.3.2. *Comparisons and affinity*

Strobili composed of lateral structures comprising bract and adaxial sporangia characterise the Chinese Lower Devonian genus *Adoketophyton* Li & Edwards, 1992. The type species, *Adoketophyton subverticillatum,* is one of the most intensively studied and most extensively known plants, including both anatomy and morphology, from the Posongchong Formation, Yunnan (Li & Edwards1992; Hao et al., 2003). It is much larger than the Sichuan material in almost all characters with sporangial complexes borne on shorter, straighter stalks that are inserted oppositely and decussately in four vertical rows (Table 2). Its terete xylem strand is centrarch. A second species, *A. parvulum* (Zhu et al., 2011), from the same formation has a similar strobilar arrangement, although complexes were much smaller than in *A. subverticillatum* in all characters but, unlike the type and Sichuan specimens, has sporangia approximately the same height as the bract. A further strobilus, preserved in part and counterpart from the Posongchong Formation was left as *Adoketophyton* sp. by Hao and Xue (2013), because of poor preservation. Sporangial complexes were reported as “borne laterally…..in 3-4 vertical rows appearing to be spirally, oppositely or sometimes randomly arranged” (p.148), but their exact positions could not be determined. Dimensions are larger, but the descriptions of the sporangial complexes including shape in lateral view, the almost sessile sporangia and the ratio of sporangial to bract height are similar. In face view the bracts are described as “long, narrow fan-shaped “, although the specimen illustrated in their figure 49 has an almost oval shape with base widening as it extends into the wide stalk. The convex sides were considered to have offered greater protection to the sporangium than that in the other species. In view of the probable differences in insertion, sporangial complex characters and the small number of specimens, Hao and Xue considered evidence too insufficient to erect a new species. We had similar reservations when attempting to compare it with the Sichuan material, but conclude that differences in bract shape and angle of insertion of the complexes set it apart from the Sichuan material and further conclude there are sufficient differences from the well established species of *Adoketophyton* to erect a new species for the Sichuan plants.

Li (1992) had placed *Adoketophyton* in the class Barinophytopsida, based on broad similarities in strobilar organisation (i.e. strobili comprising sporangia intermingling with bracts in various arrangements) and, where anatomy is known, centrarch xylem. This assignment was supported by Hao and Xue (2013) who also placed *Adoketophyton* in this class. However Kenrick and Crane (1997) prior to the discovery of anatomy had emphasised the sporangium/bract relationship and considering the latter homologous with the lycophyte sporophyll had placed the genus in a basal position in that lineage. On balance we remain of the opinion that *Adoketophyton* is best placed in the Barinophytopsida, but since members of this class require reinvestigation, leave it as *Incertae sedis.*

4.3.3. *Systematic palaeobotany*

Class: Barinophytopsida *Incertae sedis*

Genus: *Adoketophyton* Li and Edwards 1992

Type species: *Adoketophyton subverticillatum.*

*Species: **Adoketophyton pingyipuensis*** **Edwards and Li sp. nov.**

Diagnosis: Vegetative parts unknown. Parallel-side strobili at least 38mm long with sporangial complexes inserted on all sides of the strobili. Sporangial complex 4.0-6.0 mm long above junction with stalks. Stalks, 1.0-2.0 mm long and 0.4-0.5 mm wide where parallel sided, adxially curved such that complexes are held upright or slightly reflexed. Ovoid sporangia lacking stalks attached near the base of a fan-shaped bract that partially curves around sporangium and extends beyond it. Sporangia 0.9-

1.9 mm long and 0.7-0.9 mm wide. Bracts 2.3-5.0 mm long and up to 4.4 mm wide distally.

Etymology: From the name of the group from which the fossils derive

Holotype: 8534a & b.

Locality: Yanmenba section, Jiangyou district of Sichuan. 32°13.87'N, 105°10.98'E.

Stratigraphy and age: Horizon 1 in the Pingyipu Group, Lochkovian/early Pragian, Lower Devonian.

4.4. *Amplectosporangium jiangyouense* Geng 1992b; Plates IV, 6-11; V, 1-7.

4.4.1. *Description*

Re-examination of most of Geng's figured material, some of which we illustrate here and identify in the legends, together with more than 16 specimens in the collections at the Palaeobotanical Museum of China, led to the conclusion that Geng's description of terminal fertile complexes, unique to the Lower Devonian, was broadly accurate. They were composed of closely spaced dichotomous branches in which lateral sporangia were borne in rows on the inwardly-facing surfaces of the daughter branches. Here we present new information on the nature of the sporangia and the subtending stems.

The fertile stems and some of those within the terminal complexes are longitudinally ribbed (i.e. bear widely spaced striations, Plate V, 2) as are many of the sterile axes in the assemblage (Plate V, 6). Some of these ribs, where centrally spaced, may represent a conducting strand as is illustrated in the figured specimen (Plate IV, 6). Branching in the subtending stems is isotomous. Rare examples show wide angles (<100°) occurring some distance (Plate V, 4,5) below the complexes, but most stems are straight, parallel-sided and up to 70 mm long. Branching a few millimetres below the fertile region results in a pair of distinct complexes, with the size of the angle and subsequent curvature defining the overall shape of the fertile unit. Thus if the initial branching angle is acute, the overall form is tulip-shaped (Plates IV, 8, 11; V 3), if wider, goblet or fan shaped (Plates IV, 6, 10; V, 1). Despite detailed analysis, it has proved impossible to trace the fates of the individual branches in the complex due to compression, compaction and obstruction by sporangia, although an example lacking the latter was not helpful (Plates, IV, 9; V, 5). We have found at least three consecutive branch points as did Geng, but whether the subsequent branching pattern was true for all the daughter branches in the system is equivocal and, for spatial reasons, thought unlikely. Particularly intriguing is the continuation of the extreme left and extreme right branches following the initial dichotomy that lack further branching and extend to the distal extremities of the complex where they may curve inwards (Plates IV, 6, 11; V, 1). There is some indication that these axes bear sporangia on their inner surfaces and possibly in two overlapping rows indicative of superimposed branches. In other areas, and more characteristically, sporangia are borne on the inner sides of the daughter branches (Plate V, 1) as was observed by Geng, although individual sporangia are often difficult to observe because of super-positioning. Rarely is a sporangium found close to the basal dichotomy. All the sporangia we uncovered were sessile with slightly decurrent broad bases, which were slightly wider than at the mid-point (Plates IV, 8, 11; V, 1); bases were almost contiguous. Distal surfaces are rounded: rare examples are pointed (Plate IV, 11), some resulting from adpression with surrounding sporangia (Plate IV, 6). In three dimensions, each sporangium is interpreted as bluntly conical. Here we disagree with Geng, who described the sporangia as oval and borne on short stalks. Our dimensions in height are 1.2-2.3mm (n=20, x=1.9mm) are broadly similar [Geng 1.8-2.0mm long] but differ in width 0.9-3.0mm (n=21, x=1.7mm) [Geng 1.0-1.3mm wide]. We found at least three per row, again super-positioning hindered accuracy. There was little change in size towards the distal margin. The latter was sometimes marked by more or less attenuated triangular structures which Geng interpreted as sterile tips of branches (Plates IV, 6, arrowed), but rounded structures in this region may represent remains of sporangia (Plate IV, 8; V, 3). Our studies did not reveal further data on spores. Based on this new information, we have emended the generic and species diagnosis. As will be evident from the following discussion, the affinities of *Amplectosporangium* are completely unknown.

4.4.2. *Comparisons and affinities*

See section 4.7 following *Amplectosporangium* (*Oricilla*) *unilaterale* on page XX.

4.4.3. *Systematic palaeobotany*

Plantae incertae sedis

Genus: Amplectosporangium (Geng 1992) emend. Edwards and Li.

Emended diagnosis: Plant consisting of naked dichotomising axes with broadly spaced striations and terminal, fertile, closely branching systems, cup, goblet to fan-shaped in outline. Sessile sporangia borne in rows on the inside of daughter branches of the complex dichotomously branching system. Isospores trilete.

Type species: Amplectosporangium jiangyouense (Geng 1992) emend. Edwards and Li.

Emended diagnosis: Erect axes, with broad striations, at least 70mm long, 1.1-

3.3mm wide, branching dichotomous, at least twice, at angles of 30-90°, branching intervals 6.0-16.0 mm. Terminal fertile branch system consisting of incurved branches up to three times dichotomising, in a relatively short distance, to form a three-dimensional structure, tulip-, goblet- or fan-shaped in outline, 5.0-18.0 mm long by 5.0-18.0 mm wide. Incurved fertile and sterile branches 0.8-1.2mm in diameter. Sessile sporangia bluntly conical 1.2-1.3mm (x=1.9 mm long), 0.9-3.0mm (x=1.7mm) wide, borne along the inner side of incurved axes in a single row, with almost continuous bases, at least three to four per row. Spores rounded with triangular amb, 33-44μm in diameter. Simple trilete 75-80 % the length of the spore radius. Spore walls sometimes folded, covered with probable tapetal residue.

4.5*. Amplectosporangium* (*Oricilla*) *unilaterale* comb. nov.; Plate V, 8-14.

4.5.1. *Description*

All five specimens illustrated by Geng (1992a, pl. 4, figs. 28-35) and named *Oricilla unilateralis*, the genus based on North American Emsian fossils (Gensel, 1982; type *species O. bilinearis*), have been re-examined. The most extensively preserved specimens (holotype and 8340) show a fertile zone terminating a long, straight unbranched stem (1.5-2.5mm diameter, x=2.2mm, n=5), characterised by longitudinal lines dividing the surface into 4-6 strap-shaped structures. An example showing such relief occurs on one of the four fertile structures on the holotype (Plate V, 8). The stems widen slightly before bifurcating just below the sporangial zone. Each daughter branch divides again almost immediately but not synchronously and bear,on their inner margins, the lateral flattened hemispherical structures interpreted as sporangia (Plate V, 8, 9). Poor preservation prevents conclusions on the number of bifurcations and hence the number of axes bearing sporangia in the complex. At least two consecutive branches (Plate V, 14, arrows) are present in each fertile region: the upper limit is unknown. The largest complex is c. 20mm long. The complex can thus be deconstructed as comprising units in which the two products of a dichotomy each bear a single row of sporangia on the sides facing each other (8337, 8338). Plate V, 13 shows a fragment (8338) comprising two adjacent sporangia with subtending axis extending beyond the latter which may demonstrate its sterile extremity. A further unusual feature is an oval mound (c. 2.2mm high and 1.0mm wide) on the axis surface adjacent to the presumed distal margin (arrowed in Plate V, 12). Sporangia are sessile, the junction with the subtending axis being marked in some cases by a straight line which corresponds to the maximum width of the sporangium (Plate V, 10). In others, axis and sporangium form a continuous sheet (Plate V, 10, 13), and yet others, the sporangium surface is smooth but the axis marked by longitudinal striations. Sporangial outline and size are variable, even on the same or daughter branch (Table 3). It may be almost hemispherical with rounded but slightly flattened distal margin, which very rarely is marked by a very narrow (c. 0.1mm) coalified strip. Sporangia may be contiguous with their junctions at right angles to subtending axes (Plate V, 11), but where separated the narrow intervening space is a smooth concavity (Plate V, 10, 13). Sporangial size is also variable with width (w) usually greater than height (h). The following dimensions are taken from 16 examples which range from 1.5 to 4.8mm in basal width and 1.5 to 3.5mm in height. Extremes, where width is greater than height, are 4.8 x 3.5mm and 2.3 x 1.5mm and, where height is greater than width, 2.4 x 3.0mm and 2.0 x 2.5mm. Diameters of sporangial-bearing stems also are variable (0.8-2.5mm), but most are narrow.

4.5.2. *Systematic palaeobotany*

***Amplectosporangium* (*Oricilla*) *unilaterale* comb. nov. Edwards and Li**

Plantae incertae sedis

Genus: Amplectosporangium Geng 1992

Type species: *Amplectosporangium jiangyouense* Geng 1992

Comb. nov: *A. unilaterale* (syn. *Oricilla unilateralis* Geng 1992)

Diagnosis: Plant at least 75mm tall comprising naked parallel-sided unbranched stems terminating in fertile complexes at least 20mm long. Stems 1.5-3.5mm wide with longitudinal lines, producing strap-shaped appearance which extends into the fertile complex. Complex comprises at least two consecutive dichotomously branching axes; branching in daughters asynchronous, lateral sporangia borne on inside of each dichotomy. Sporangia sessile, broadest attachment, c. hemispherical in outline, margin marked by unthickened narrow border (c. 0.1mm diameter). Sporangial bases contiguous or narrowly spaced. Sporangial basal width 1.5-4.8mm, height 1.5-3.5mm. Dehiscence and spores unknown.

Basionym: *Oricilla unilateralis* Geng 1992a. Studies in the Early Devonian flora of Sichuan. Acta Phytotaxonomica Sinica 30, 197-211; pl. 4, figs. 28-35.

Holotype: 8337. Geng, 1992a,

Locality: Yanmenba section, Jiangyou district of Sichuan, 32º13.87'N, 195º10.98'E.

Stratigraphy and age: Horizon 1 the Pingyipu Group, Lochkovian/early Pragian (Lower Devonian).

4.6. *Amplectosporangium* (*Oricilla*) *unilaterale* forma *minor*; Plate V*,* 15-17.

4.6.1. Description

A single specimen preserved in part and counterpart (Plate, V ,15,17) has terminal sporangial complexes resembling those of *A. unilaterale*, but differs in a number of characters. Compared with the latter, the vegetative axes are slender with at least three consecutive branches with wide branching angles similar to those in *A. jiangyouense*, and bear the surface striations found in both species of *Amplectosporangium*. The diameter of the stem (2.7mm) below the first isotomy approximates to those of the latter, but in daughter branches, immediately above the first isotomy, branches are much narrower (1.5mm) and after further branching are c. 0.7mm wide below the fertile region. The overall length of the specimen is 35mm. Unfortunately, the terminal complexes are distorted (Plate V, 17), and the counterpart is not an exact replica of the part because one of the subtending axes has been uncovered. However sporangia are of similar shape to those of *A. unilaterale* if slightly smaller (Table 4) and are linearly arranged on one side of a branching axis. Very limited evidence suggests that branching within the complex was limited. The specimen is thought closest to *A. unilaterale*, but more branched and with simpler sporangial complexes. It shares with *A. jiangyouense*, sporangial shape and insertion and vegetative characters. On such limited evidence, we are reluctant to erect a further species but leave it as a further form of that species, namely *Aplectosporangium unilaterale* forma *minor* the epithet reflecting the dimensions of the stems in the fertile regions.

4.7. *Identification and affinities*

Gensel (1982) erected the genus, *Oricilla,* on well preserved specimens with fertile and sterile regions. The latter showed dichotomous branching, circinate tips and bore enations. Sporangia borne on short stalks in two opposite rows but not in strobili were described as reniform, isovalved, with equivocal marginal thickenings. Junctions between sporangia and stalks were not clear, the latter leaving the stems at right angles or slightly inclined distally. Sporangia were usually preserved in full valve view. More recently Hao and Xue (2013) described specimens from the Posongchong Formation in Yunnan with smooth isotomously branching stems bearing occasional lateral reniform sporangia on short stalks borne again not in strobili but in one or two opposite vertical rows both above and below branching points. Dehiscence was into two equal valves lacking thickened borders. They distinguished the Chinese material from the Canadian (*O. bilinearis*) on stem size and sporangial features and from Geng's *O. unilateralis* on sporangial arrangements, before leaving their specimens as *Oricilla* sp. On the basis of the unique sporangial morphology of the Sichuan material and terminal, branched fertile complexes, we exclude it from *Oricilla.*

Amplectosporangium jiangyouense (Geng 1992b) as described above also has a complex crowded multisporangiate branching structure terminating isotomously/ dichotomously branching smooth stems with broad striations with oval sporangia borne laterally to the inside of the daughter branches of a dichotomy with up to four sporangia in each row. This arrangement closely resembles the units in *Oricilla unilateralis* as described here. Differences noted from our revised concept account of *Amplectosporangium jiangyouense* relate to sporangial shape and attachment, and in the compactness and number of branches in the complex. However, we consider there are sufficient similarities to transfer *Oricilla unilateralis* into that genus as a new combination—*Amplectosporangium unilaterale.*

The affinities of both taxa remain conjectural. These condensed, branched, reproductive complexes terminating naked, relatively unbranched stems set

Amplectosporangium apart from other taxa in the Sichuan assemblage and, indeed, from coeval and younger plants elsewhere. The gross morphology of the basic unit of the complex viz. a single row of closely set, lateral sporangia, is reminiscent of the strobilus of a *Platy-zosterophyllum* (e.g. Croft and Lang, 1942), but the clustering of the units in a condensed branching structure plus sporangial shape and attachment features set *Amplectosporangium* apart. In summarising the composition of the Silurian Pingyipu assemblages, Hao and Xue (2013) noted that the fertile structures in *Amplectosporangium* were similar to those in *Eophyllophyton*, the latter possessing rows of lateral sporangia on a branching 'leaf'. Earlier in the book, on the basis of their cladistical analysis, they had erected a new class in the Euphyllophytina, the Eophyllophytopsida, sister to all other groups. Its single genus *Eophyllophyton* bore both paired branching laminate leaves and laminate branching structures with rows of stalked lateral sporangia, reniform to circular in face view with possible distal dehiscence. The sporangia were inserted on the inside of the branches which curved over them, forming unique fertile complexes, just 2.3-3.4mm wide. Those in *Amplectosporangium* are solitary, much larger, lack laminae but share a similar 'bau plan'. The lack of anatomy in the Sichuan material is particularly frustrating as demonstration of a centrarch xylem strand would provide further evidence for relationship with *Eophyllophyton* and other euphyllophytes.

Catenalis digitata from the Lower Devonian Posongchong Formation in Yunnan merits consideration (Hao and Beck, 1991). The smooth stems with marked longitudinal striations and wide branching angles are terminated by much narrower isotomously branching structures, they were termed fertile branchlets, because each bears a single row of dorsiventrally compressed, contiguous, sessile sporangia. Branching was interpreted as in one plane, resulting in a fan-shaped architecture in life. Hao and Beck's 1991 reconstruction of the plant reflects their conclusion, based on 'axial functional structure' and environments of deposition, that it was an aquatic or semi-aquatic. This was elaborated further by the detailed study of the lithological associations in the Posongchong Formation (Hao and Xue, 2013) where it was the sole plant taxon in a thin black shale and thinly-bedded mudstones in the Chanputang section and associated with the occasional *Lingula,* often considered an indicator of brackish water. Deposition was thought to have occurred in a quiet environment, possibly close to the shore line of a lagoon.

Finally, *H.corymbosa* (Cookson, 1935) with terminal fertile complexes comprising dichotomously branching axes each terminating in an elongate sporangia might seem an inappropriate plant for comparison with *Amplectosporangium.* Detailed analysis of the branching patterns within the terminal complex of the now considered Lower Devonian fossils by Cookson showed that, while in certain specimens branching was at the same level and the daughters grew equally to produce sporangia at the same level, in others one sporangium was produced close to the branching point but the outer daughter branch overtopped the inner before ending in a sporangium. However the tips of the complex appeared always at the same level because the inner sporangium was longer than the outer. In some instances the outer branch was sterile. Further, the 'lateral' overtopped sporangia sometimes occurred at different levels within the complex. *Hedeia* would thus seem to represent an intermediate grade of organisation but nowhere as complex as in *Amplectosporangium*.

5. General considerations

Our aim in undertaking this study was to clarify the characteristics of the plants with lateral sporangia aggregated into strobili in the Sichuan assemblages to provide accurate identification leading to relationships. As is typical of most palaeobotanical investigations, such activity led to further avenues of research which in turn are essential prerequisites for rigorous phylogenetic and palaeogeogeographical studies. These include the need to:

a) target taxa within the basal lycophytes / Zosterophyllopsida including, for example, the genus *Zosterophyllum* itself (where anatomical data are sparse), prior to further cladistical analyses (Kenrick and Crane, 1997; Hao and Xue, 2013), and those taxa (and assemblages), which bias palaeophytogeographic reconstructions. Here examples would be *Margophyton goldschmidtii* (Zacharova, 1981; Schweitzer, 1989), which featured strongly in the detection of diversity patterns in Devonian palaeogeography by Cascales-Miñana and Meyer-Berthaud (2015), plus an in depth revision of the Siberian assemblages;

b) revisit the frequently overlooked barinophytes, resolved in cladistic analyses as basal in the lycophytes with *Barinophyton* itself in the zosterophylls (Kenrick and Crane, 1997; Crane et al., 2004) with very far reaching implications for the evolution of the sporangium/sporophyll complex. The group is undoubtedly paraphyletic, but united in the possession of strobili in which sporangia are variously associated with bracts. While the heterosporous Upper Devonian representative, *Barinophyton citrulliforme* had an exarch protostele (Brauer, 1980), in two homosporous Lower Devonian examples, *Krithodeophyton* (Edwards, 1968) and *Adoketophyton* (Hao et al., 2003), the protoxylem is central in a terete strand. While perhaps overemphasising the significance of xylem differentiation, this character sets the older taxa apart from other barinophytes and the Lycophytina. The diversity of bract/sporangial relationships requires revision, but in *Adoketophyton*, the adaxial insertion of the sporangium close to the base of the expanding bract (but not in an axillary position) is quite clear and was considered as representing an intermediate stage leading to the evolution of the typical lycophyte organisation by Crane and Kenrick (1997, figure 5). An alternative explanation in the light of anatomical differences is that the complex might demonstrate convergence relating to nutrition and protection of sporangia in a plethora of lineages associated with the radiation of early tracheophytes;

c) review the palaeogeographic relations of the Sichuan assemblages in the light of findings reported here. All species are restricted to the locality. At the generic level, only *Zosterophyllum* is cosmopolitan, *Adoketophyton* is also recorded in Yunnan, while *Amplectosporangium* and *Ornicephalum* are restricted to Sichuan, thus providing further evidence for the preponderance of endemicity in Chinese Lower Devonian vegetation while reinforcing differences between the assemblages in the two Chinese provinces. However comprehensive palaeogeographic analysis require the inclusion of taxa with enations which were originally described by Geng (1992a) and which are currently being reinvestigated.

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Plate captions

Plate I. 1-7) *Zosterophyllum ovatum* sp. nov. 1) Unbranched naked stems with basal parts of strobili. Most sporangia in full face new; laterally compressed sporangia in strobilus on extreme left. Specimen 8322 (figured in Geng 1992a, pl. 1, fig. 3). Scale bar = 10mm. 2) Counterpart of holotype (as designated by Geng 1992a). Strobili with widely separated sporangia, except for example on far left with closely inserted folded sporangia. Arrow indicates sporangium magnified in 3). Specimen 8321b (figured in Geng 1992a: pl. 1, fig. 2). Scale bar = 10mm. 3) Sporangium in face view with narrow border (arrow) and stalk, magnified from 2). 4) Strobilus magnified from 2). Scale bar = 2mm. 5), 6) Laterally compressed sporangium on short stalks, enlarged from left hand strobilus in 1). Scale bars = 2μm. 7) Incompletely preserved sporangium, distal part missing. Arrowed treble lines may indicate slight displacement of two valves. Specimen 8321b. Scale bar = 2μm.

Plate II. 1-10) *Ornicephalum (Zosterophyllum) sichuanense* gen et sp. nov. All specimens originally described and figured by Geng 1992a, pl. 2. 1) Base of strobilus terminating straight stem; specimen incomplete at both ends. Specimen 8323a (figured in Geng, 1992a, pl. 2, fig. 10). Scale bar = 5mm. 2), 3) Lateral sporangia, enlarged from 1). Small black arrows show possible abaxial extension of stalk into sporangium. White arrows indicate dehiscence line. Scale bars = 2mm. 4) Counterpart of sporangium in 2). Arrow indicates feature possibly associated with departure of another sporangium into the matrix. Specimen 8323b. Scale bar = 2mm. 5) Cellular pattern enlarged from abaxial valve in 3). Scale bar = 500μm. 6) Fragment of strobilus with four sporangia, the two in profile badly preserved. White spot on left hand sporangium is a needle mark. Specimen 8325 (figured in Geng, 1992a, pl. 2, fig. 14). Scale bar = 5mm. 7), 8) Two sporangia enlarged from 6). Arrows indicate dehiscence features. Scale bars = 2mm. 9) Fragment of strobilus. Holotype. Arrow indicates possible adaxial valve, abaxial valve missing. Specimen 8324b. Scale bar = 2mm. 10) Counterpart of partial strobilus of holotype. Specimen 8324a. Scale bar =

2mm. **11-14) *Adoketophyton pingyipuensis* sp. nov.** Parts of sporangial complexes enlarged from strobilus figured in Plate III. Specimen 8534a and b. Scale bars = 1mm. 11) Sporangium with possible dehiscence line (arrows) attached to base of bract (from Plate III,2) 12) Sporangium partially covered by bract (from Plate III,1) 13) Lower part of bract removed to reveal abaxial margin of sporangium (from Plate III,1). 14) Face of bract partially exposed. Arrow indicates remains of sporangium (from Plate III, 2).

Plate III. *Adoketophyton pingyipuensis* sp. nov. 1), 2) Part and counterpart of holotype. Specimen 8534a and b. Scale bar = 5mm.

Plate IV. 1-5) *Adoketophyton pingyipuensis* sp. nov*.* 1), 2) Part and counterpart of iron-stained strobilus, compression/impression with some relief. Unequivocal sporangia not observed. PEPB00039. Scale bar = 10mm. 3) – 5) Views of bracts enlarged from 1) after some uncovering. 3) Almost complete bract in face view. 4) Partially uncovered bract. 5) Folded laterally compressed bract tapering into stalk. **6–11) *Amplectosporangium jiangyouense* Geng.** 6) Weathered specimen showing typically crowded arrangement of sporangia and axes. Note the dark lines continuing from stem into fertile regions, these are of similar dimensions to the ribs that characterise the subtending axes, but could also represent vascular strands. Arrow indicates sterile tip. (8357, Geng, 1992b, pl. I, fig. 2). Scale bar = 5mm. 7) Holotype of *A. jiangyouense* so designated in Geng 1992b, pl. I, fig. 1. Specimen somewhat deteriorated, such that individual axes and sporangia cannot be distinguished. Specimen 8356. Scale bar = 10mm. 8) Heavily coalified complex with limited branching and rows of sporangia. 8255. Illustrated by Geng 1992b, pl. II, fig.

2). Scale bar = 5mm. 9) Terminal complex branching system lacking sporangia by with gross morphology similar to fertile examples with major basal dichotomy. Little coalified material remained. 8258. Illustrated by Geng, 1992b, pl. II, fig. 5. Scale bar = 5mm. 10) Iron-stained impression with little detail, arrow indicates possible sporangia and stars, the sterile distal projections presumably of the branching axes. 8358. Illustrated by Geng, plate 1, fig. 5. Scale bar = 5mm. 11) Heavily coalified complex of similar organisation to that in 8) with well-defined sporangia with rounded to attenuated apices. Specimen 8275. Scale bar = 2mm.

Plate V. 1-7) *Amplectosporangium jiangyouense* Geng. 1) Typical complex with uncovered broad-based sporangia. PEPB00040. Scale bar = 2mm. 2) Axis with ribbing below complex in 1). Scale bar = 2mm. 3) Highly weathered complex indicate tips of possible sporangia. PEPB00041. Scale bar = 5mm. 4) Poorly preserved fertile specimen showing proximal wide-angled isotomy proximally and narrower distal isotomy with daughter branches terminating in fertile complexes. 8359. Illustrated by Geng 1992b, pl. I, fig. 6. Scale bar = 10mm. 5) Dichotomously branching specimen with terminal cluster of sterile branching axes. PEPB00042. Scale bar=10mm. 6) Sterile branching system assigned to *Amplectosporangium* based on wide branching angles in ribbed axes. PEPB00043. Scale bar = 10mm. 7) Sterile tip after further development of Plate V, 1. Scale bar = 1 mm. **8-14) *Amplectosporangium* (*Oricilla*) *unilaterale* comb. nov.** 8) Surface with four aligned axes each terminating in fertile complex. The most complete (on right) shows a tuning fork arrangement with rows of sporangia borne on inner surface of axis, illustrated by Geng, 1992a as holotype of *Oricilla unilateralis*, pl. 4, figs. 28, 29. 8337. Scale bar = 5mm. 9) Typical simple forking unit. 8339. Scale bar =4mm.10), 11) Fragments of fertile axes. 8341, PEPB00043. Scale bars = 2mm. 12) Contorted fragment on reverse of holotype. Scale bar =5.5mm. 13) Possible tip (figured by Geng, 1992a, pl. 4, fig. 31). Specimen 8338. Scale bar = 5mm. 14) Fragment with branch points. 8340.**15-17) *Amplectosporangium unilaterale* forma *minor*.** Part and counterpart. Arrow indicates vascular strand. PEPB00044a, b. Scale bars = 5mm. 16) Magnification of fertile region of 15). Scale bar = 5mm.

Table 1. *Ornicephalum sichuanense*. All dimensions in mm.

Table 2. Comparisons of dimensions, in millimetres, of four species of *Adoketophyton*. Data on *A. subverticillatum* from Li and Edwards (1992) and Hao et al. (2003), and those of *A. parvulum* from Zhu et al., (2011) and tabled in Hao and Xue (2013). *A.* sp. described in Hao and Xue (2013). * taken just above sporangium and derived by doubling width as assumed to be folded.

Table 3. Dimensions in mm of specimens placed in *Amplectosporangium unilaterale.*

Table 4. Comparisons of the three *Amplectosporangium* taxa (dimensions in mm).

Specimen	Overall length	Axis width	Strobilar axis width	Stalk		Sporangium height			Maximum width	Dehiscence length
				length	width	total	distal	proximal		
					b-m					
8323	60	1.7-1.8		1.8	0.9-0.8	1.8	-	-	2.4	1.5
			1.3	1.5	0.9-0.6	2.0	-	-	1.6	1.3
8324	48	1.5-1.7	0.5-1.5	4.2	0.7	1.5*			1.2*	-
				3.5	0.7-0.8	1.9			2.5	-
				3.5	0.6-0.9	1.5			2.5	-
				3.0	0.7	1.6			2.0	
				2.4	0.7	1.5			2.0	
				2.6	0.6-1.0	2.0			2.8	
8325	16	0.8	0.9-1.1	2.3	0.3-1.1	2.4	2.0	0.4	2.6	1.5
		0.6-1.1		?	0.6-1.1	2.7	2.2	0.5	2.8	1.5

Table 1. *Ornicephalum sichuanense*. All dimensions in mm. b=base,

m=midpoint,*=incomplete.

	Sporangial axis	Sporangial basal width	Height	Axes
8338	1.2-1.4	3.4	2.0	
		3+	2.5	
8340	(nothing compete) 2.5	4.5	2.7	2.0→4.0 below spike
	2.5		2.0	
PEPB00043	absent	2.1	1.2	
		2.1	0.9	
		2.2	1.2	
		2.3	1.1	
8341	v. narrow/broken	2.2	1.5	
		3.4	2.3	
8339	0.3-0.8	3.5+	2.2	
		3.4	2.4	Axes 1.3-2.5 (x=2.2, n=5)
		5.0	2+	
		4.3	2.0	
8337		4.0	2.0	2.5
		c. 4.0	1.6	2.5
		7.0		2.0→3.5
		4.5	3.0	
	(	2.0	2.5	
	1.5 RH (	2.4	3.0	116
	(	1.5	1.5	1.5-2.2
	LH	4.8	3.5	
		4.6	3.0	
	2.0-3.5	3.5	2.1	
		4.0	2.6	

Table 3. Dimensions in mm of specimens placed in *Amplectosporangium (Oricilla) unilaterale.*

Characters	Measurements in mm	*A. subverticillatum*	*A. parvulum*	*A.* sp. *B***	*A. pingyipensis* sp. nov.
Axes	Width of main axes	0.9-2.6	0.8-1.7	1.2-2.1	?
Strobili	Length	90 (maximum)	7-17	>95	>38
Bracts	Length	3.2-10.0	1.5-2.1	4.0-6.8	2.3-5.0
	Width	3.6-8.4	1.7-2.5	2.1-3.0	<4.4
Stalks	Length	0.5-1.3	0.5-0.7	1.2-1.8*	0.7-1.5
	Width	-	-	0.5-0.7	0.4-0.5
Sporangia	Height	1.5-2.7	0.7-1.1	1.5-1.8	0.9-1.9
	Width	2.0-3.2	0.8-1.5	1.8-2.2	0.7-0.9
	Length of stalks	0.05-0.7	0.2	?	N/A
	Width of stalks	0.1-1.4	0.2	?	N/A

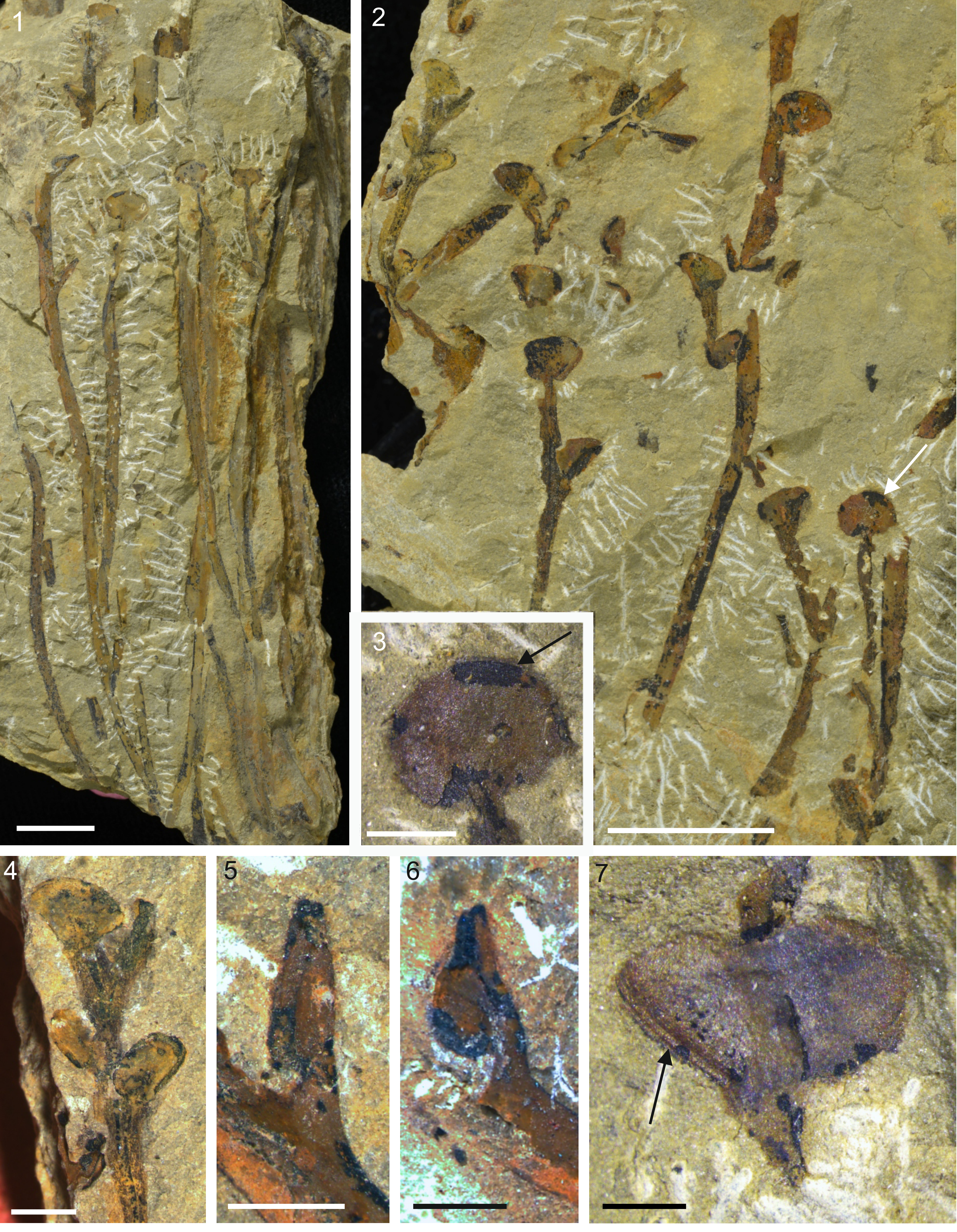
Table 2. Comparisons of dimensions, in millimetres, of four species of *Adoketophyton*. Data on *A. subverticillatum* from Li and Edwards (1992) and Hao et al. (2003), and those of *A. parvulum* from Zhu et al., (2011) and tabled in Hao and Xue (2013). **A. sp. described in Hao and Xue (2013). *taken just above sporangium and derived by doubling width as assumed to be folded.

	Maximum sporangial width	Sporangial height	Stem width from base to distal complex
Amplectosporangium jiangyouense here	1.0-1.3	1.8-2.0	2.0 → 2.5
Geng (1992b)	0.9-3.0	1.2-2.3	
A. unilaterale	1.5-4.8	1.5-3.5	→ 2.5
A. unilaterale forma *minor*	1.8-3.6	1.0-2.0	2.7 → 0.7

Table 4. Comparisons of the three *Amplectosporangium* taxa (dimensions in mm).

Geng, 1992a, b	These investigations	Locality level	Affinity	Distribution
Eogaspesiea gracilis	Identification unreliable	Horizon 1	?	*
	Jiangyounia gengi Edwards and Li, (submitted)	Horizon 1	R	SE
	Polycladophyton gracilis Edwards and Li, (submitted)	Horizon 1	R	SE
Zosterophyllum myretonianum	*Z. ovatum* sp. nov. this paper	Horizon 1	Z	CGSE
Z. yunnanicum	Not studied		Z	CGSE
Z. sichuanensis	*Ornicephalum sichuanense* gen. nov. this paper		Z	SE
	Guangnania minor (Edwards et al., 2016)	Horizon 3	Z	ChE
Hicklingia cf. *edwardii*	*Baoyinia sichuanensis* Edwards and Li, (submitted)	Horizon 2	Z	SE
-	*Sichuania uskielloides* Edwards and Li, (submitted)	Horizon 1	Z	SE
-	*Adoketophyton pingyipensis*, this paper	Horizon 1	B	ChE
Amplectosporangium jiangyouense	*A. jiangyouense*, emended this paper	Horizon 1	?	SE
Oricilla unilateralis	*Amplectosporangium* (*Oricilla*) *unilaterale*, this paper	Horizon 1	?	SE
-	*A. unilaterale forma minor,* this paper	Horizon 1	?	SE
Zosterophyllum longa (Wang, 2007)	*Yanmenia* (*Zosterophyllum*) *longa*, Edwards et al., 2016	Horizon 1	?	SE
Drepanophycus spinaeformis	Under investigation		L	
spinosus			L	
D. sp.			L	
Leclerqia complexa		Horizon 3	L	

Table 5. Results of the revision of the Sichuan assemblages. SE=Sichuan endemics; Ch= Chinese endemics; CGSE=Cosmopolitan genus-Sichuan endemic species; Cosmopolitan genus- Chinese endemic species: CS= cosmopolitan species.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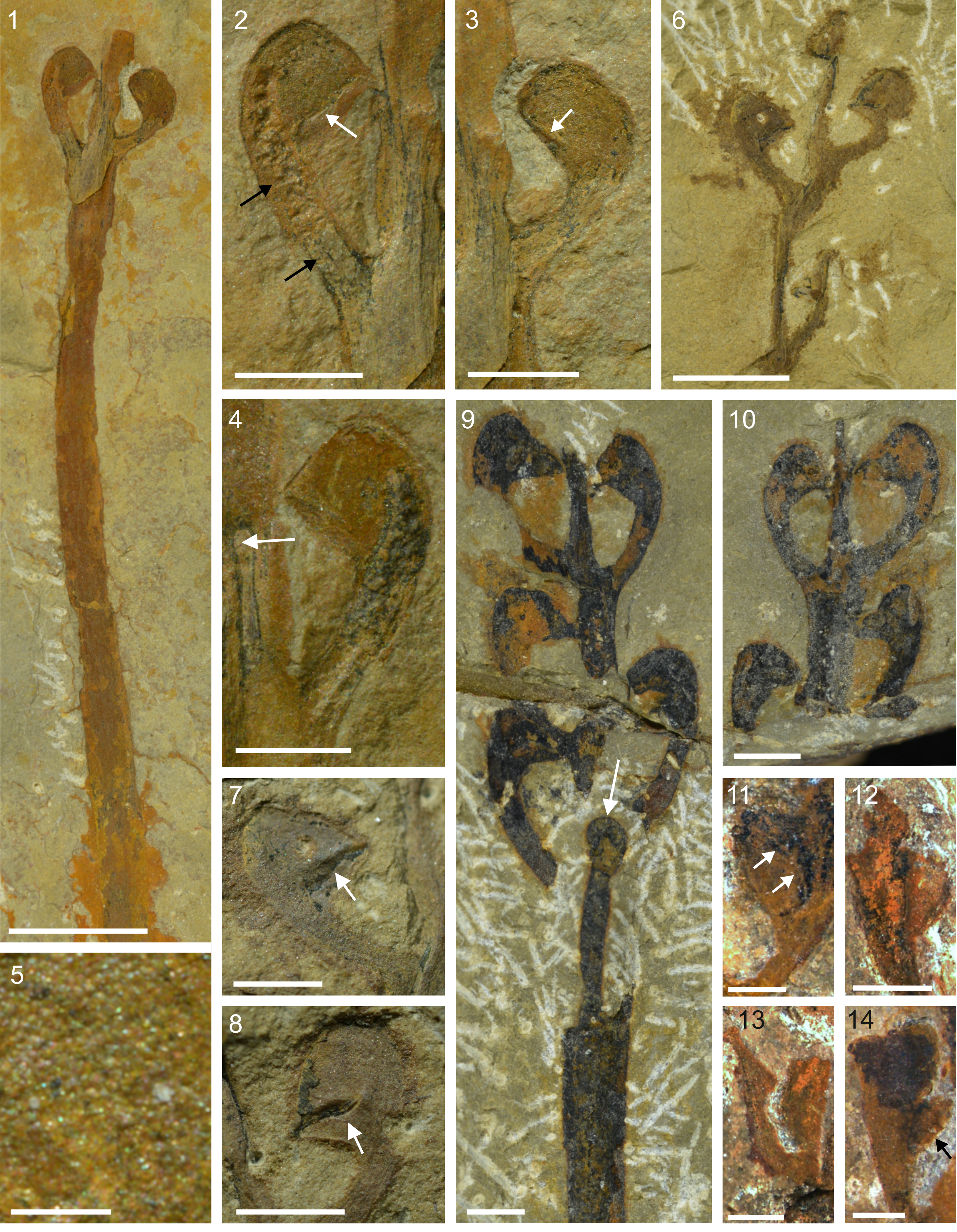
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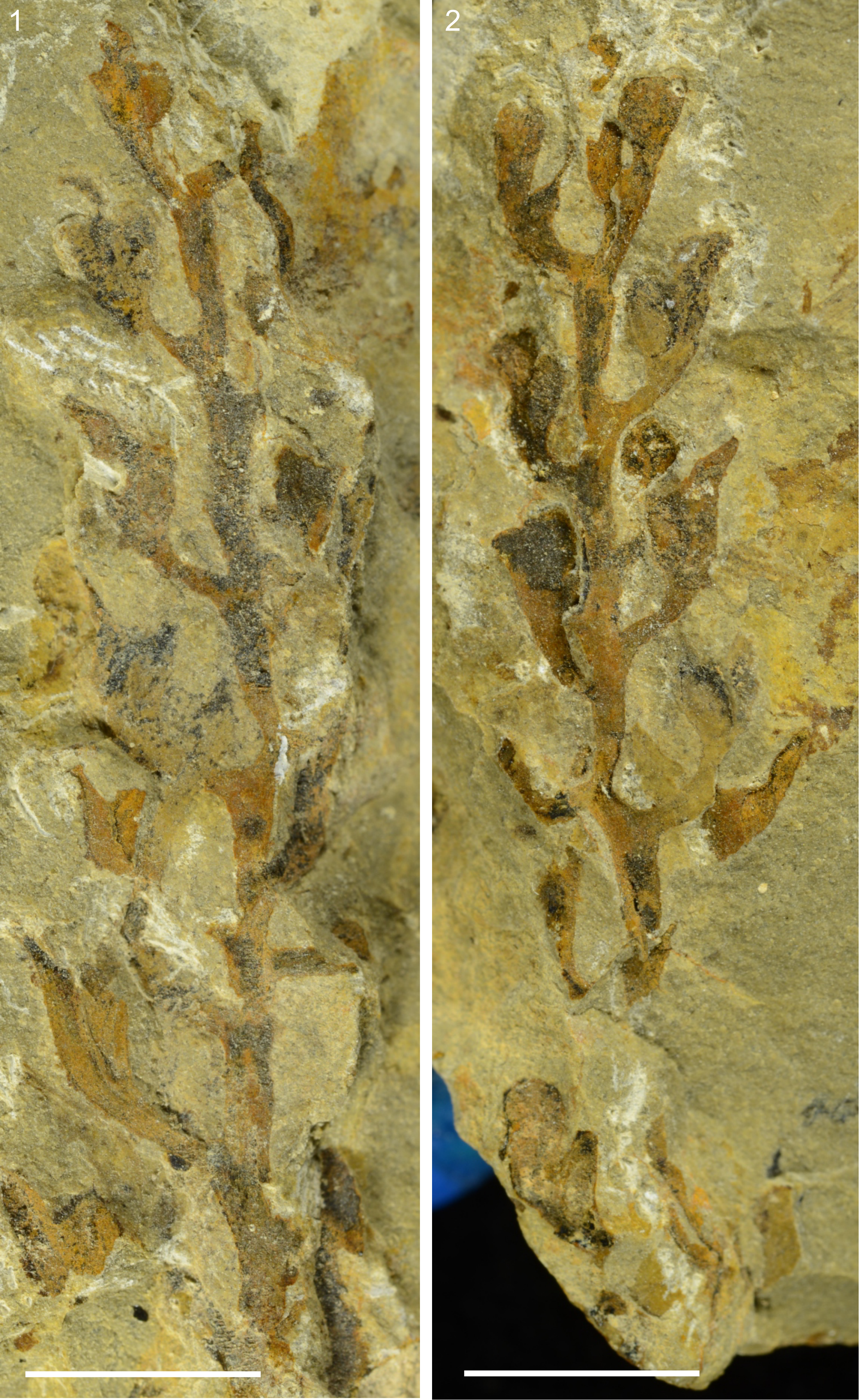
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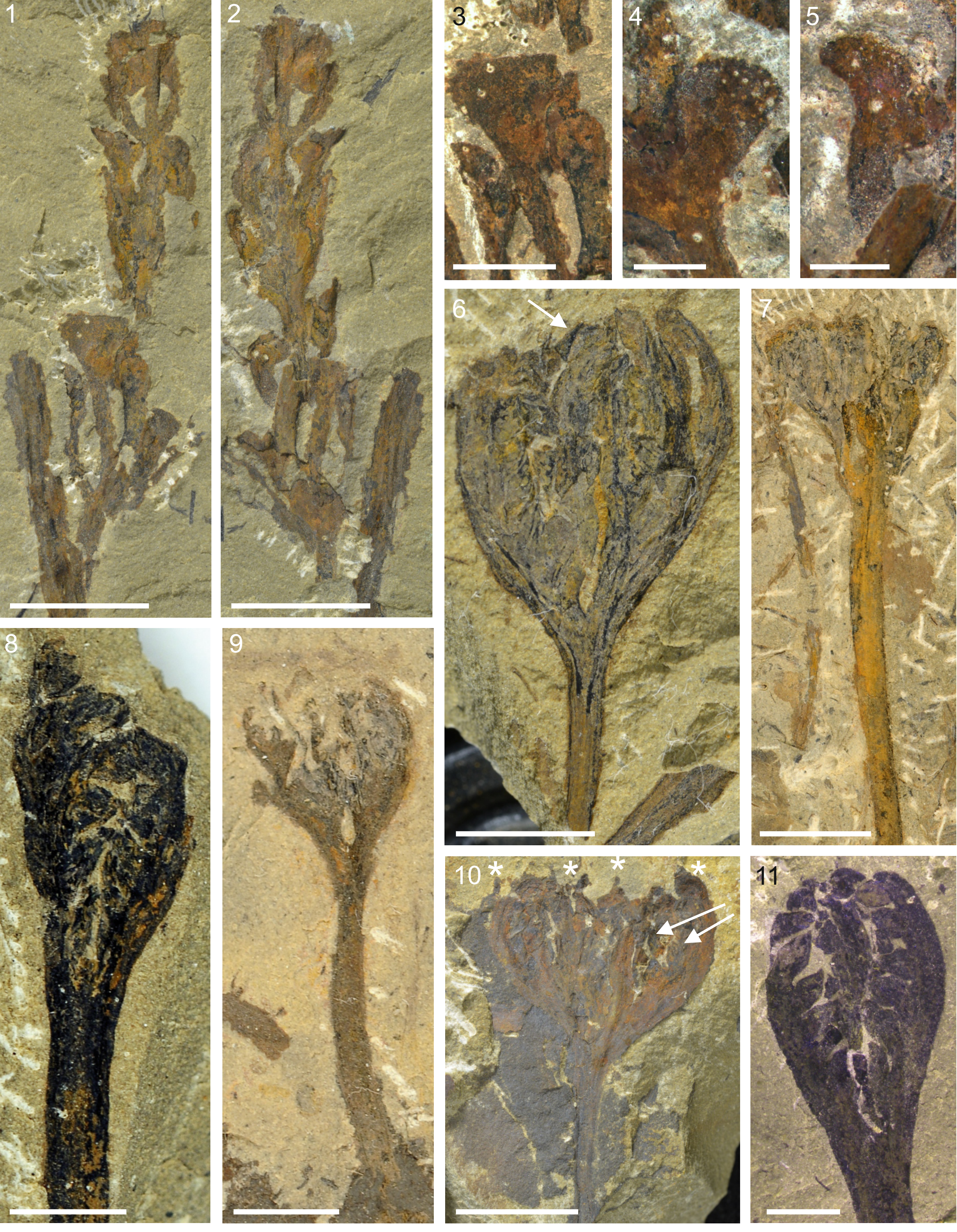
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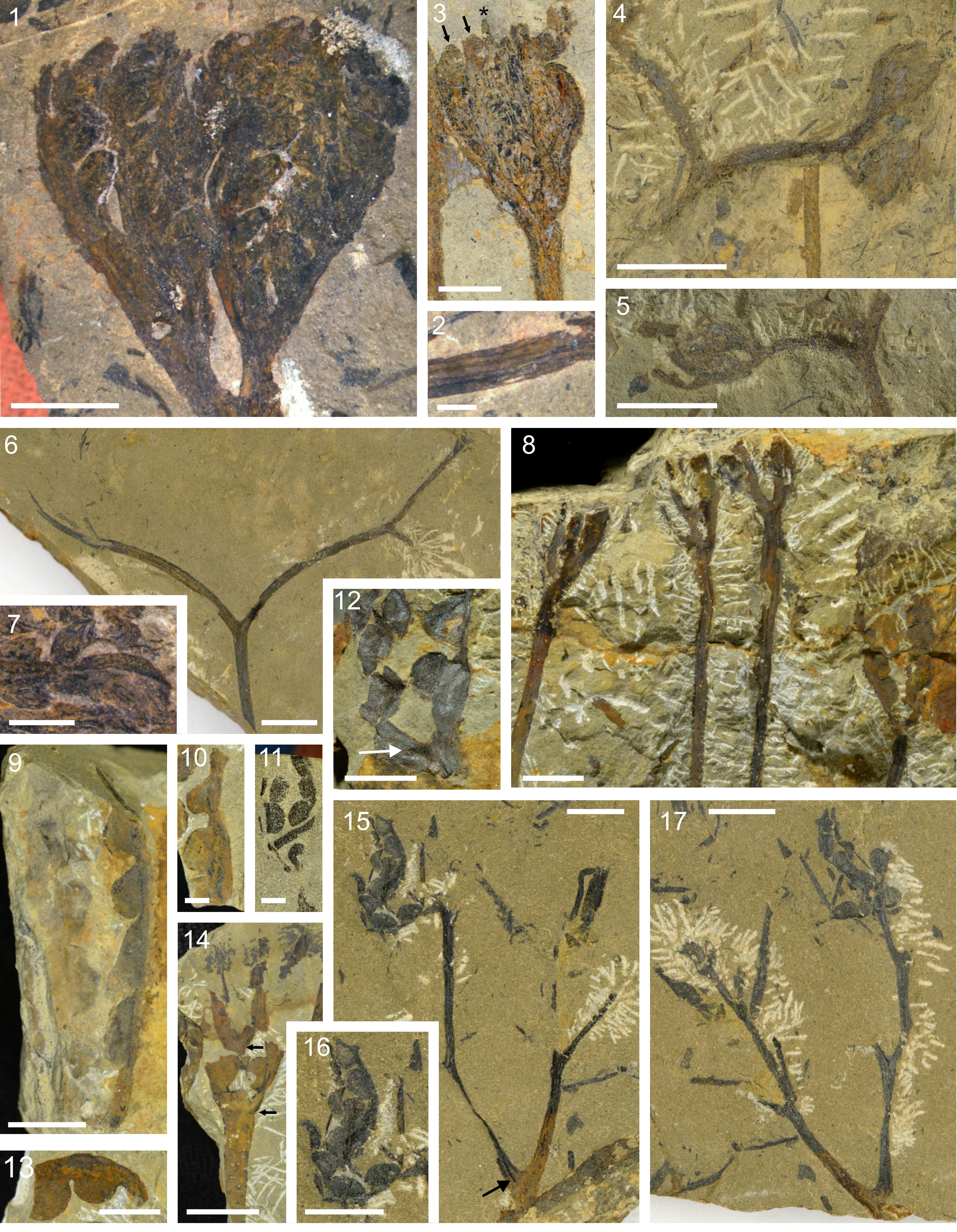
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