Keraphyton gen. nov., a new Late Devonian plant genus of iridopterid affinities from New South Wales, Australia

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Abstract

Iridopterids are early diverging fern-like plants closely allied to the sphenopsids, a group represented today by the genus *Equisetum*. They have been documented in Middle to early Late Devonian deposits of Laurussia and Xinjiang. Their Gondwanan record is poor, with occurrences limited to Venezuela and Morocco. Here we describe a new genus from a late Late Devonian locality of New South Wales. It is represented by a single anatomically preserved large stem characterized by a star-shaped vascular system with protoxylem strands located at rib tips, and by a lack of secondary tissues. This stem differs from all other known iridopterid axes by the division pattern of its vascular system. *Keraphyton mawsonii* gen. et sp. nov. adds a new record of early fern-like plants in a poorly known Late Devonian flora of Australia. It also supports the view that this flora was, at least, partly specific to this part of the world at this time.

Introduction

The Devonian is a time of major interest for understanding the origination and early phases of evolution of two major groups of plants, the ferns and the seed plants. Many analyses have focused on the early seed plants and their unique mode of reproduction, and a reasonable level of understanding of their patterns of diversification has been reached (Taylor, Taylor & Krings, 2009; Meyer-Berthaud, Gerrienne & Prestianni, 2018 and references herein).

This is not the case for the early representatives of the ferns and their allies, i.e., the sphenopsids, cladoxylopsids, and iridopterids, which are not well circumscribed in the fossil record and whose phylogenetic relationships are not fully understood (Rothwell & Nixon, 2006; Taylor, Taylor & Krings, 2009; Cordi & Stein, 2005; Meyer-Berthaud, Soria & Young, 2007; Xue, Hao & Basinger, 2010). Beck & Stein (1993) suggested that the extinct cladoxylopsids and iridopterids which thrived during the Middle and Late Devonian, together with the sphenopsids which have extant representatives, may have been part of a natural group united by the possession of "permanent protoxylem" strands. Later, Kenrick & Crane (1997) recognized this character as the synapomorphy of a more extended clade, the Moniliformopses or sphenopsid-fern clade, which also included the Filicopsida. The relevance of the Moniliformopses has been heavily discussed (Pryer et al., 2001; Rothwell & Nixon, 2006). The discovery of new Devonian fossils affiliated to the sphenopsids and the iridopterids suggests that a close phylogenetic relationship between these taxa remains a plausible option (Xue, Hao & Basinger, 2010).

The Iridopteridales were identified by Stein (1982) as plants characterized by a unique set of derived features including a whorled organotaxis, two types of lateral organs potentially borne at the same nodes - ultimate appendages and branches, the lack of secondary tissues, and an actinostele, i. e., a star-shaped column of primary vascular tissues. Six genera were referred to the Iridopteridales by Berry & Stein (2000). Three were based on anatomically preserved specimens, *Asteropteris* Dawson 1881, *Arachnoxylon* (Read) Stein, Wight & Beck 1983, and *Iridopteris* (Arnold) Stein 1982. Two were represented by specimens preserved both as compressions and in anatomy, *Ibyka* Skog & Banks 1973 and *Compsocradus* Berry & Stein 2000. The compression-based genus *Anapaulia* Berry & Edwards 1996, which resembles *Ibyka*, was also included in the Iridopteridales. The genus *Rotoxylon* Cordi & Stein 2005 was later added to this order despite its lack of an actinostelic vascular system (Cordi & Stein 2005).

In this paper, we describe a new iridopteridalean plant genus of Late Devonian age from the locality of Barraba in New South Wales, one of the rare localities of this age in eastern Australia to have provided anatomically preserved plant fossils of excellent quality (Chambers & Regan, 1986; Meyer-Berthaud, Soria & Young, 2007; Evreïnoff et al., 2017). We further discuss the significance of this discovery in relation to the stratigraphical and palaeogeographical occurrences of the Iridopteridales.

Materials & Methods

The present paper is based on a single specimen collected by Mr. John Irving at Barraba, in the New England region of New South Wales, Australia. It is part of a collection of anatomically preserved specimens discovered by this amateur geologist on the left bank of the Manilla River at Connors Creek crossing. The fossils occur in the Mandowa mudstone, a formation of the Tamworth Belt consisting of a thick sequence of dark laminated mudstones interbedded with thin layers of creamy siltstones and sandstones (Vickery, Brown & Percival, 2010). These marine sediments correspond to a distal shelf and continental slope environment. The beds containing plants are Famennian (Late Devonian) in age (Wright, 1988).

The 90 mm long specimen representing *Keraphyton* is housed in the Geological Survey of New South Wales and referenced under number MMF 44986. To avoid fragmentation we embedded it into a low viscosity two components epoxy resin (Araldite® AY103/HY991) before sectioning it into five blocks (A to E). We prepared eight transverse sections, one on each cutting face (AS, BI, BS, CI, CS, DI, DS and EI), and two longitudinal sections in block A (AL1 and AL2). The specimen is not well preserved distally. The following description is based mainly on sections made in blocks A and B.

Thin-sections were observed with an Olympus SZX12 stereomicroscope and an Olympus BX51 microscope. We used the Archimed and Olympus cellSens imaging software packages for acquiring numerical photographs and measuring cells. We used the AutoStitch image stitching software for reconstructing fine resolution images from multiple photos (Brown & Lowe, 2007). The drawing in Figure 2A was made with a camera lucida fixed on the stereomicroscope.

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~~*Keraphyton:*~~

~~*Keraphyton mawsonii:*~~

Systematic palaeobotany

Class CLADOXYLOPSIDA Pichi-Sermolli, 1959
Order IRIDOPTERIDALES Stein, 1982
Family INCERTAE SEDIS
Genus *KERAPHYTON* gen. nov.

Type species. *Keraphyton mawsonii* Champreux, Meyer-Berthaud, Decombeix sp. nov.

Derivation of name. From κέρας (kéras), the ancient greek for horn. The generic name, *Keraphyton*, refers to the horn-shaped outline of the primary xylem ribs of the stem in transverse section.

Diagnosis. As type species, see below:

KERAPHYTON MAWSONII sp. nov.

Diagnosis. Stem up to 20 mm in diameter, with primary tissues only. Vascular system actinostelic, consisting of four fundamental ribs united to a central segment. Fundamental ribs branching unequally, one branch dividing into two equal ultimate ribs, the other dividing in more ultimate ribs of distally decreasing dimensions. Protoxylem strands exarch to mesarch, at tip of ultimate ribs. Metaxylem tracheids from 20 to 140 µm in diameter, the largest ones in the midplane of the ribs. Tracheid walls showing scalariform to multiseriate bordered pit pairs with elliptical apertures. Endodermis-like cells consisting of rectangular cells up to 200 µm high and 120 µm periclinally. Inner cortical cells up to 160 µm in diameter, thin-walled, polygonal to circular in transverse section, with transverse to oblique endwalls in longitudinal section. Outer cortex homogeneous, with cells becoming thicker-walled and narrower towards periphery.

Holotype. Specimen MMF44986, Palaeontological reference collections, Geological Survey of New South Wales, Australia.

Type locality. Barraba, New England, New South Wales, Australia; left bank of the Manilla River, upstream from the Connors Creek crossing.

Stratigraphy. Mandowa mudstone Formation, Parry Group, Tamworth Belt. Famennian, Upper Devonian.

Derivation of name. In honor of Prof. Ruth Mawson, distinguished Australian palaeontologist who was interested in all aspects of fossil life, and was a delightful leader of palaeobotany-palaeontology field trips to Devonian localities of north-eastern Australia.

Description

The Barraba specimen is a straight, 90 mm long and 20 x 10 mm wide portion of stem (Fig. 1A). It has been compressed and is slightly fluted throughout its length. There is no external evidence of any branch or lateral organ.

The stem contains only primary tissues and is actinostelic (Fig. 1B). Some parts of the xylem at rib tips, as well as the phloem and associated tissues, are poorly preserved and replaced by a lacuna containing dark material. The inner cortex is made of thin-walled cells that merge progressively to the thicker-walled elements of the outer cortex. All cortical cells are elongated in longitudinal section. The outermost cortical layers and epidermis are missing. One side of the specimen at least is surrounded by a dark amorphous material that may have resulted from the degradation of the outermost cell layers. No vascular trace is observed at any level in this specimen.

Stele

The primary xylem is deeply ribbed in transverse section (Figs. 1B and 2A). Using Stein's (1982) nomenclature, it consists of four fundamental ribs united by a central segment about 2.5 mm long (Figs. 1C and 2B). The fundamental ribs bifurcate unequally (Figs.B, 1D and 2B), one branch being extended and producing three or four ultimate ribs of unequal length (Figs 1E, 1G and 1H), the second branch being shorter and dividing into two ultimate ribs approximately equal in dimensions (Figs. 1D and 1F). The four systems of at least six ultimate ribs (Ia, Ib, IIa, IIc in Fig. 2C) produced by the fundamental ribs are organized in two opposite pairs (pairs I and II). The two systems of a pair (e.g., Ia and Ib) exhibit a 180° rotational symmetry. The fundamental ribs range from five to ten cells and are 400 to 500 µm wide (Fig. 1C). Those subtending pair I rib systems are about 3.5 mm long, those subtending pair II rib systems are shorter; the reconstructed length of the latter, after adding their broken parts, is about 2 mm (Figs. 1B and 2C).

Metaxylem tracheids are polygonal with rounded corners in transverse section (Figs. 3A, 3B, 3C and 3D). They measure up to 140 µm in diameter. The largest ones are located in the midplane of the ribs (Figs. 3A and 3C). The smallest tracheids are 20-35 µm wide and arranged in 1-2 layers along the lateral edges of the ribs (Fig. 3C). There is no protoxylem strand in the central segment nor in the fundamental ribs (Figs. 3A and 3C). Protoxylem strands are exarch to mesarch at the tips of the ultimate ribs (Figs. 3B and 3D). They are not associated with any thin-walled cell nor lacuna. In longitudinal section, tracheid walls show elongated bordered pit pairs which are either uniseriate (i.e., scalariform) or multiseriate (Figs. 4A and 4B). Apertures are elliptical.

The pyrite-filled lacuna surrounding the xylem is about 200 µm wide. It may attain a width of 1,000 µm around rib tips and contain patches of preserved cells in these areas. We tentatively interpret groups of small (14-38 µm wide) thin-walled elements as fragments of phloem tissue (Fig. 3H).

Cortex

On its inner side, the cortex is bounded by one to two layers of cells with a rectangular shape in transverse section (Figs. 3E, 3F and 3H). They may represent an endodermis. These cells are 50 to 120 µm in the periclinal dimension and 30-75 µm radially. In longitudinal section they show transverse end-walls and their height ranges from 80 to 200 µm (Fig. 4A).

The inner cortical cells are laterally compressed (Fig. 3E). When their original shape and size are preserved, these thin-walled elements appear polygonal to circular in transverse section (Figs. 3C and 3G), and elongated with transverse to oblique end-walls in longitudinal section (Fig. 4C). Some are filled with pyrite. They measure 35-160 µm in diameter and are 90-400 µm long.

The outer cortex is homogeneous. Outer cortical cells show progressively smaller diameters and thicker walls towards the stem periphery (Fig. 3G). Diameter decreases from 140 to 25 µm and wall thickness increases from about 7 to 18 µm outwardly. In longitudinal section, the shape and length of the outer cortical cells do not differ much from those of the inner cortical cells (Fig. 4D). Numerous small oval to circular holes on the walls may represent pits or early signs of degradation.

Vascular traces and organotaxis

There is no evidence of vascular trace emission in the best preserved parts of the specimen but the structure of the primary xylem as illustrated in Figures 1B and 2 provides some information on the organotaxis. The ultimate ribs produced by the two long branches of pair I rib systems are comparable in size (Figs. 1D and 1H). They look more elongated than those of pair II (Figs. 1E, 1G and 2C), a pattern that may be linked to the emission of incipient traces in the former rib systems. How exactly each rib system contributed to the vascular supplies of lateral organs and how many types of lateral organs were borne at each node is highly conjectural. The stelar organization of *Keraphyton mawsonii* as summarized in Figure 2C, however, is suggestive of an opposite decussate arrangement of the lateral organs.

Discussion

Affinities

There is no information on the lateral organs, their nature, size and arrangement in *Keraphyton*. Nevertheless this stem provides sufficient features to demonstrate its uniqueness and its affiliation to a new genus within the "permanent protoxylem" group proposed by Beck & Stein (1993).

Based on developmental hypotheses involving the role of hormones in the differentiation of the primary vascular tissues, Beck & Stein (1993) distinguished two main groups among the numerous plants of Devonian and early Carboniferous age characterized by an actinostelic vascular system. In the "radiate protoxylem" group which includes some basal euphyllophytes, such as the Stenokoleales, the aneurophytalean progymnosperms, and some earliest seed plants, protoxylem strands occur along the midplanes of the xylem ribs and they all derive by branching from a single permanent strand located centrally. In the "permanent protoxylem" group, protoxylem strands are exclusively peripheral, a pattern that may reflect an hormonal prominence of the shoot apex compared to the hormonal influence of the lateral organs. With its protoxylem strands located only at rib tips and its largest tracheids occupying the midplane of the ribs, *Keraphyton* is clearly a member of the "permanent protoxylem" group which encompasses the Sphenophyllales, the Iridopteridales, and the pseudosporochnalean and non-pseudosporochnalean cladoxylopsids.

Five sphenophyllalean genera of Late Devonian age are represented by specimens that are partly or entirely preserved in anatomy. These are *Sphenophyllum* Brongniart 1828, *Eviostachya* Stockmans 1948, *Hamatophyton* (Gu & Zhi) Wang, Hao, Tian & Xue 2006a, *Rotafolia* (Wang, Hao & Wang) Wang, Hao, Wang & Xue 2006b, and probably *Pleurorhizoxylon* Zhang, Berry, Wang, Xue & Liu 2018 (Zhang et al., 2018; Terreaux de Felice, Decombeix & Galtier, 2019). Axes in these small-sized plants differ from *Keraphyton* by a simpler stele which shows only three undivided short lobes. In the genus *Rotafolia*, the stele may occasionally be tetralobate, but here again, lobes are short and undivided (Wang et al., 2006b). The actinostele in *Keraphyton* is built on a four-arm pattern with much more extended ribs. Sphenophyllalean axes do not exceed 10 mm in diameter. Despite their small size, and unlike the *Keraphyton* type-specimen, they often show a well-developed secondary xylem.

The Pseudosporochnales, and the non-pseudosporochnalean cladoxylopsids such as *Cladoxylon* Unger 1856, *Polyxylon* (Read & Campbell) Chambers & Regan 1986, and *Pietzschia* Gothan 1927, are characterized by a dissected stele composed of a much higher number of xylem ribs than *Keraphyton* (Taylor, Taylor & Krings, 2009). Some ribs may temporarily connect internally, forming U-, V- or W-shaped patterns in transverse section but, unlike that of *Keraphyton*, the stele is never stellate with all ribs permanently connected at their inner extremity.

Within the "permanent protoxylem" group, *Keraphyton* shares the largest number of characters with the Iridopteridales (Stein, 1982; Berry & Stein, 2000). First, *Keraphyton* contains only primary tissues. Since Stein's (1982) diagnosis mentioning this character, species such as *Arachnoxylon minor* Stein, Wight & Beck 1983 and *Rotoxylon dawsonii* Cordi & Stein 2005*,* which occasionally show a secondary-type of xylem consisting of radially aligned tracheids and even rays, have been recognized as iridopteridalean (Stein, Wight & Beck, 1983; Cordi & Stein, 2005). Despite its relatively large diameter, the *Keraphyton* stem is devoid of any tissue of this type and is more consistent with the original concept of the order as defined by Stein (1982). Second, the primary vascular system of *Keraphyton* consists of a deeply ribbed column of vascular tissue showing radially oriented xylem ribs that are united centrally. These characters also match the original definition of the Iridopteridales. Third, the wall ornamentation of the metaxylem tracheids of *Keraphyton,* which consists of scalariform and circular bordered pits with elliptical apertures, is similar to that recorded by Stein (1982) for the order.

There is no lateral organ attached to the type-specimen of *Keraphyton* and its anatomical preservation does not allow the analysis of its organotaxis via the pattern of emission of the vascular traces. The shape of the stele and the paired organization of the fundamental rib systems, however, suggest that the lateral organs were not produced helically. Iridopterids are characterized by the production of several lateral organs at the same node. For the *Keraphyton* stem, we suspect that, whatever their nature and number at each node, lateral organs were borne in an opposite decussate arrangement, a pattern consistent with the organotaxis in the Iridopteridales.

Keraphyton is characterized by specific features that set it aside from all other iridopteridalean taxa known to date and justify its assignation to a new genus (Fig. 5). The *Keraphyton mawsonii* type-specimen is one of the largest iridopterid axes known to date. It is comparable in diameter to the type-specimens of *Asteropteris noveboracensis* and *Rotoxylon dawsonii*. Its primary vascular system, however, is markedly different (compare Fig. 5O with Figs. 5I and 5Q). Contrary to *Keraphyton*, the fundamental ribs of *Rotoxylon* are undivided, and a few ones only are centrally connected. The stele of *Asteropteris* shows no symmetry and the fundamental ribs, before division, are much shorter. The vascular system of *Keraphyton* differs also from that of the largest specimens of *Metacladophyton* (Wang & Geng) Wang & Lin, 2007, a genus of Givetian to early Frasnian age represented by two species from Hubei. *Metacladophyton* is not included in the iridopterid-sphenophyllalean group recognized in Xue et al.'s (2010) cladistic analysis but it has been proposed as a possible representative of the Iridopteridales by Berry and Stein (2000). In *Metacladophyton*, stelar ribs are not connected centrally (Figs. 5E, 5G and 5N). A temporary connection of the stelar ribs has been observed in small axes only (Fig. 5F). The largest axes differ from *Keraphyton* not only by a different stelar configuration but also by the possession of a large amount of a secondary-type of xylem surrounding the stelar ribs (compare Fig. 5O with Figs. 5G and 5N).

Fundamental ribs in the Iridopteridales divide equally forming two or three ultimate ribs of similar dimensions. This is the case in *Iridopteris* (Fig. 5A and 5B), *Asteropteris* (Fig. 5I), *Arachnoxylon* (Figs 5C, 5D, 5J, 5K and 5L), *Compsocradus* (Fig. 5H), *Asteropteris* (Fig. 5I), *Ibyka* (Fig. 5M) (Bertrand, 1913; Skog & Banks, 1973; Stein, 1982; Stein, Wight & Beck, 1983; Berry & Stein, 2000). This is also the case in *Denglongia* (Xue & Hao) Xue, Hao & Basinger 2010 (Fig. 5P), an actinostelic genus that has not been assigned to any specific order but whose possible iridopterid affinities have been investigated (Xue, Hao & Basinger, 2010). On the contrary, fundamental ribs of *Keraphyton* divide asymmetrically, resulting in the short and long branches reported above. The stelar ribs of *Keraphyton* are thinner and more extended radially than those of any other known iridopterids. Protoxylem strands in *Keraphyton* are less conspicuous than in the other iridopteridalean taxa, they look exarch in some ultimate ribs, and they are not associated with lacunae. Finally, the maximum diameter of metaxylem tracheids are up to 140 µm wide, a diameter that largely exceeds that of the other iridopteridalean species which rarely reaches 100 µm.

Palaeogeographical and stratigraphical considerations

The Iridopteridales, comprised of the genera *Asteropteris*, *Arachnoxylon*, *Iridopteris*, *Ibyka, Compsocradus,* and *Anapaulia* range from the upper Eifelian (Middle Devonian) to the Frasnian (early Late Devonian). They are recorded from Laurussia (eastern USA and Spitzbergen), Gondwana (Venezuela and Morocco), and Xinjiang (Bertrand, 1913; Berry & Edwards, 1996; Skog & Banks, 1973; Stein, 1981, 1982; Stein, Wight & Beck, 1983; Berry & Stein, 2000; Fu et al., 2011). Despite its dissected stele with numerous unconnected stelar ribs, the addition of *Rotoxylon* Cordi & Stein, 2005 to this list of iridopterids does not change the stratigraphical and palaeogeographical ranges of the order.

The genus of Frasnian age from Hubei, *Denglongia,* is characterized by an actinostelic vascular system which shows many similarities with that of the Iridopteridales (Xue, Hao & Basinger, 2010). The only anatomical difference lies in the possession of two protoxylem strands in the rib tips which are enlarged. This enlargement is suggestive of the initiation of a division of the tip, a common process in the iridopterids. Our opinion, therefore, is that this anatomical difference is minor and that iridopterids conforming to the original concept of the order may well have been present in South China during the Frasnian time interval.

The youngest genus showing some iridopterid characters is *Serripteris* Rowe & Galtier, 1989, represented by a single specimen of Tournaisian (Early Carboniferous) age from southern France. *Serripteris* has an actinostelic vascular system. Its stele has a very simple shape and shows four undivided ribs, each one with a single permanent protoxylem strand at its tip (Fig. 5R). *Serripteris*, however, differs from the Iridopteridales in its helical arrangement of the lateral branches and lack of ultimate appendages at nodes (Rowe & Galtier, 1989). At this state of knowledge, the iridopterid affinities of *Serripteris* are uncertain and a stratigraphical occurrence of the Iridopteridales in the Carboniferous speculative.

It is clear from these considerations that, up to now, genera conforming to the original description of the Iridopteridales (Stein, 1982) ranged in time from the Eifelian to the Frasnian. They occurred in Laurussia, Xinjiang, and probably South China. Their Gondwanan record is poor and only comprised of *Compsocradus* from Venezuela (Berry & Stein, 2000) and *Anapaulia* from both Venezuela and Morocco (Berry & Edwards, 1996; Prestianni et al., 2012). *Keraphyton* is the first representative of the Iridopteridales reported from Australia. Its occurrence in the Famennian beds of the Mandowa mudstone at Barraba supports the view that the stratigraphical range of the Iridopteridales went beyond the Frasnian and encompassed, at least, the whole Late Devonian. Moreover, *Keraphyton* expands the palaeogeographical range of the Iridopteridales to the easternmost part of north Gondwana.

At the Barraba locality *Keraphyton* is associated with numerous axes of *Leptophloeum australe* preserved as adpressions together with anatomically preserved specimens of the lycopsid *Cymastrobus irvingii,* the non-pseudosporochnalean cladoxylopsid *Polyxylon australe*, and wood fragments referable to the archaeopteridalean progymnosperm genus *Callixylon* (Chambers & Regan, 1986; Meyer-Berthaud, Soria & Young, 2007; Evreïnoff et al., 2017). *Leptophloeum australe* and *Callixylon* were cosmopolitan taxa in the Late Devonian but *Cymastrobus*, *Polyxylon autrale,* and now *Keraphyton* have not been recorded elsewhere, supporting the distinctiveness of at least part of the vegetation in eastern Australia at this time.

Conclusions

We describe a new genus of fern-like plants, *Keraphyton* gen. nov., from a Famennian locality of north-eastern New South Wales, Australia. It is represented by a large anatomically preserved stem showing iridopteridalean characters. This discovery shows that the Iridopteridales spanned the whole Late Devonian and occurred in the far east of Gondwana. After *Polyxylon australe*, a species from the same locality affiliated to the cladoxylopsids, this is the second report of an early diverging fern-like plant in the late Late Devonian of eastern Gondwana. *Keraphyton mawsonii* and *Polyxylon australe* are unknown elsewhere, supporting the distinctiveness of at least part of the Australian flora during the Famennian.

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Figure 1

Keraphyton mawsonii gen. et sp. n., holotype. General features.

(A) Specimen before preparation. (B) General view of stem. (C) Central segment and four fundamental ribs. (D) Rib system Ib showing short branch dividing into two equal ultimate ribs at right and long branch producing at least three long ultimate ribs at left. (E) Long branch of rib system IIa producing short ultimate ribs. (F) Short branch of rib system IIa dividing into two ultimate ribs. (G) Long branch of rib system IIb producing short ultimate ribs. (H) Long branch of rib system Ia producing long, but broken, ultimate ribs. cs: central segment; fr: fundamental rib, la: lacuna, ic: inner cortex, oc: outer cortex, lb: long branch, sb: short branch. All views except (A) from transverse section MMF 44986 BI1. All scale bars except (B) 500 µm, (B) 2 mm.

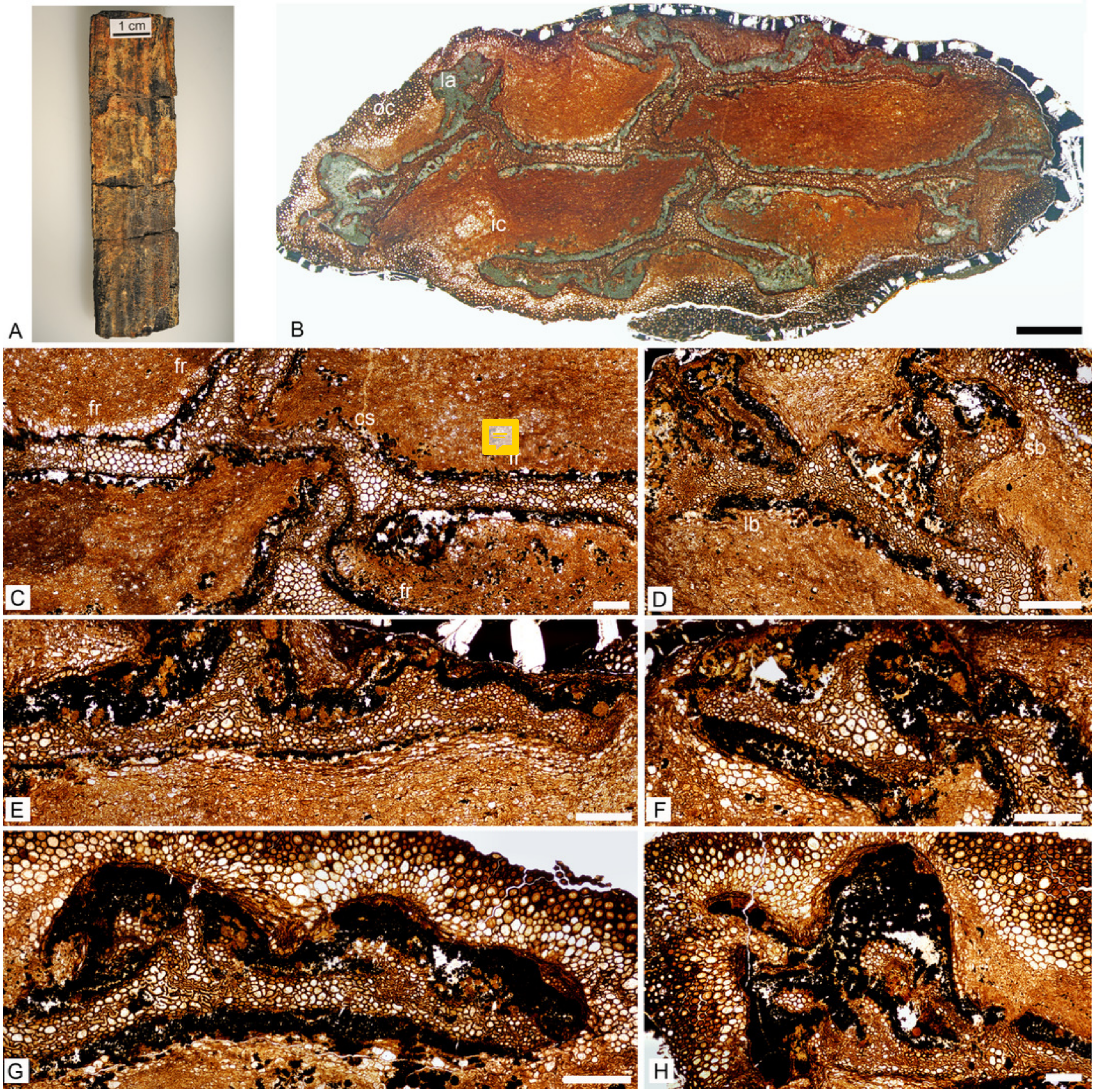

1 cm
A
oc
la
lc
B
fr
fr
cs
fr
fr
C
sb
lb
D
E
F
G
H

Figure 2

Keraphyton mawsonii gen. et sp. n., holotype.

(A) Drawing of specimen in transverse section; xylem in dark grey, cortex in light gray. (B) Schematic outline of xylem. (C) Interpretation of xylem structure.

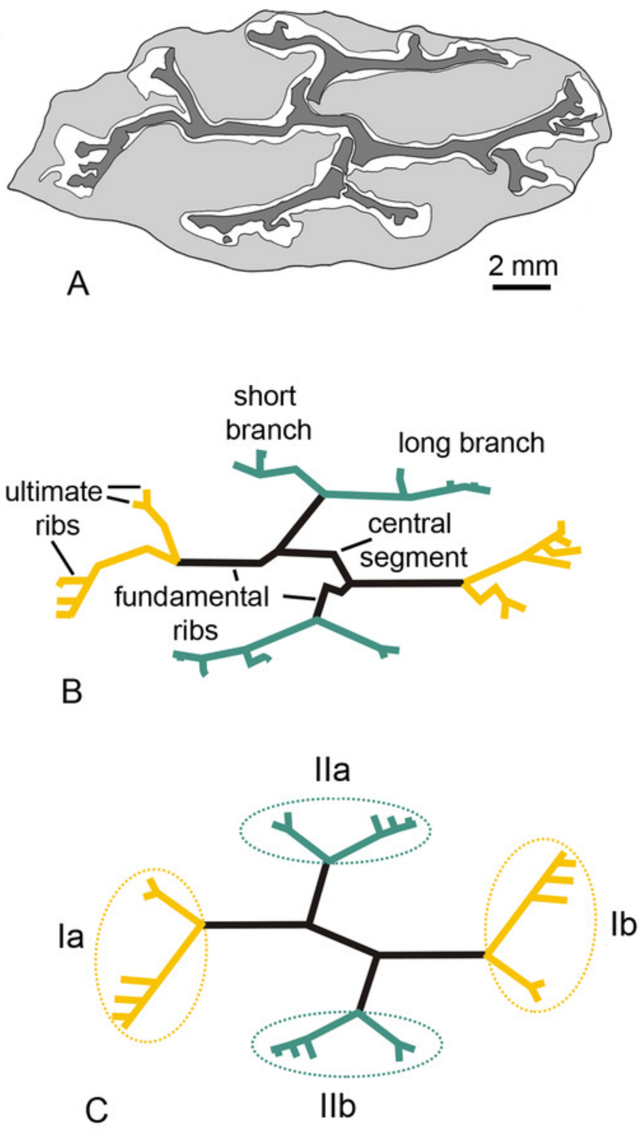

2 mm
A
short branch
long branch
ultimate ribs
central segment
fundamental ribs
B
IIa
Ia
Ib
IIb
C

Figure 3

Keraphyton mawsonii gen. et sp. n., holotype. Detailed anatomy in transverse section.

(A) Central segment showing wide tracheids in the median plane, even in the most compressed zones. (B) Tip of ultimate rib showing small tracheids interpreted as elements of exarch to mesarch protoxylem strand. (C)Fundamental rib showing wide tracheids in the median plane and small ones on lateral edges; well-preserved inner cortical cells at top. (D) Tip of ultimate rib showing small tracheids interpreted as elements of exarch to mesarch protoxylem strand. (E) Endodermis-type cells bordering highly compressed inner cortical cells; displaced xylem tracheids at left. (F) Endodermis-type cells. (G) Section through cortex showing large, thin-walled inner cortical cells at right and small, thick-walled outer cortical cells at left. Transition is not abrupt. (H) Lacuna around ultimate rib tip showing presumable remains of phloem tissue; endodermis-type cells at top. En: endodermis-type cells, la: lacuna, ph: phloem tissue, ic: inner cortex, oc: outer cortex. All views except (D) from transverse section MMF 44986 BI1, (D) from transverse section MMF 44986 CI1. All scale bars 200 µm.

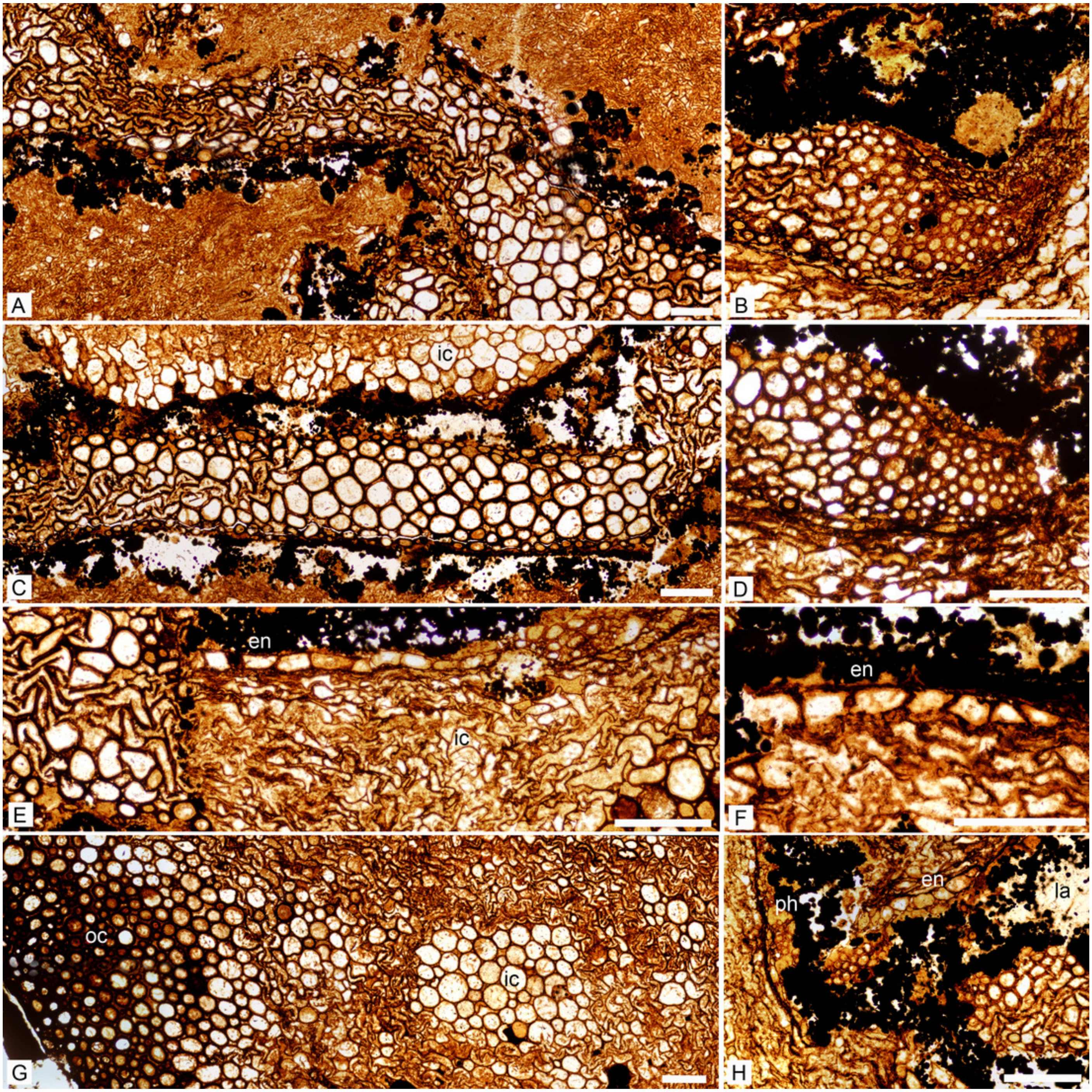

A
B
ic
C
D
en
ic
E
en
F
oc
ic
G
ph
en
la
H

Figure 4

Keraphyton mawsonii gen. et sp. n., holotype. Detailed anatomy in longitudinal section.

(A) Section showing from left to right tracheids, lacuna and endodermis-type cells, highly compressed inner cortical elements and elongated thick-walled outer cortical cells. (B) Xylem tracheids showing elongated bordered pits with elliptical apertures. (C) Inner cortical cells with transverse end walls (D) Outer cortical cells with progressively smaller diameters and thicker walls to the right. Note small holes in the cell walls. En: endodermis-type cells, la: lacuna, ic: inner cortex, oc: outer cortex. All views from transverse section MMF 44986 ASl1. All scale bars 200 µm.

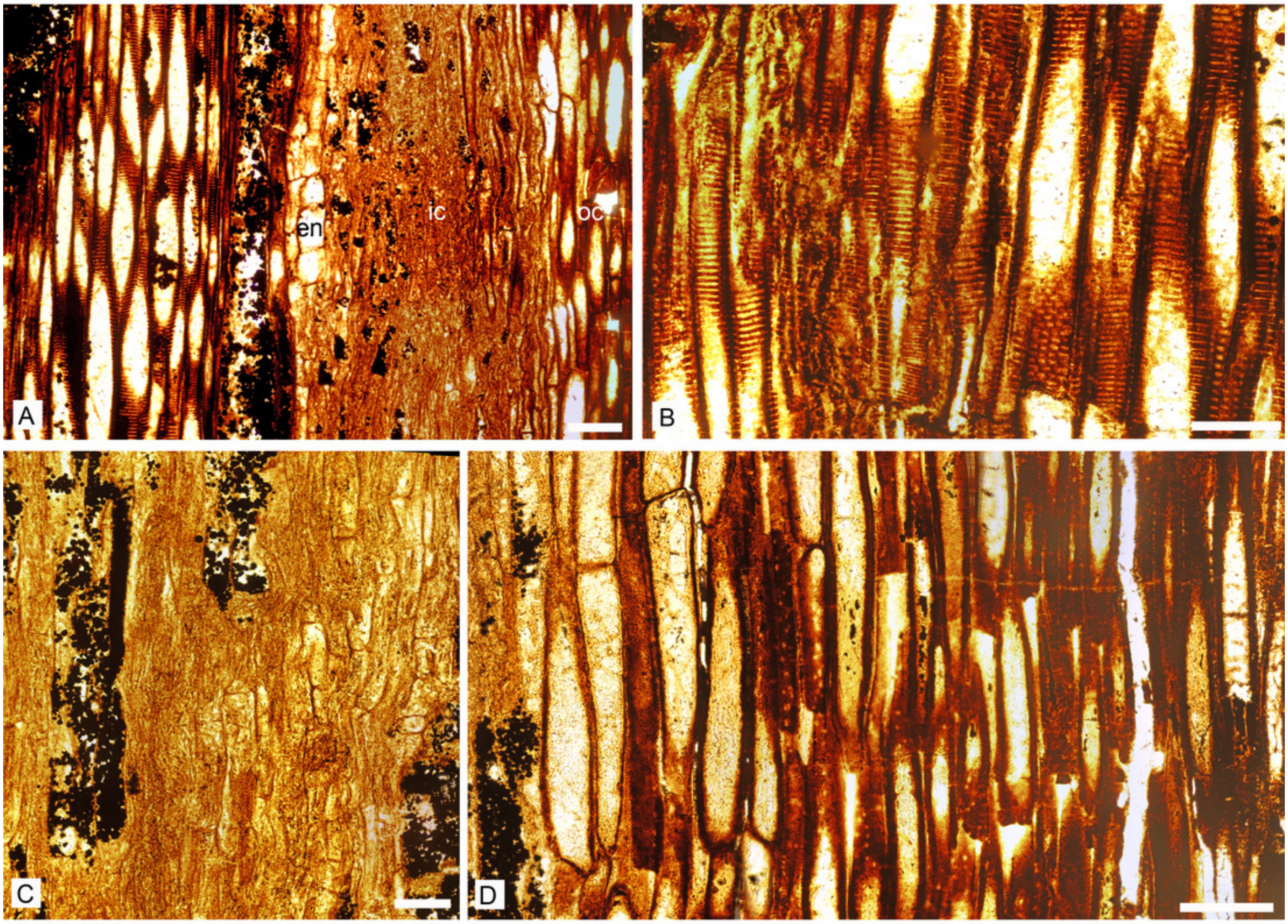
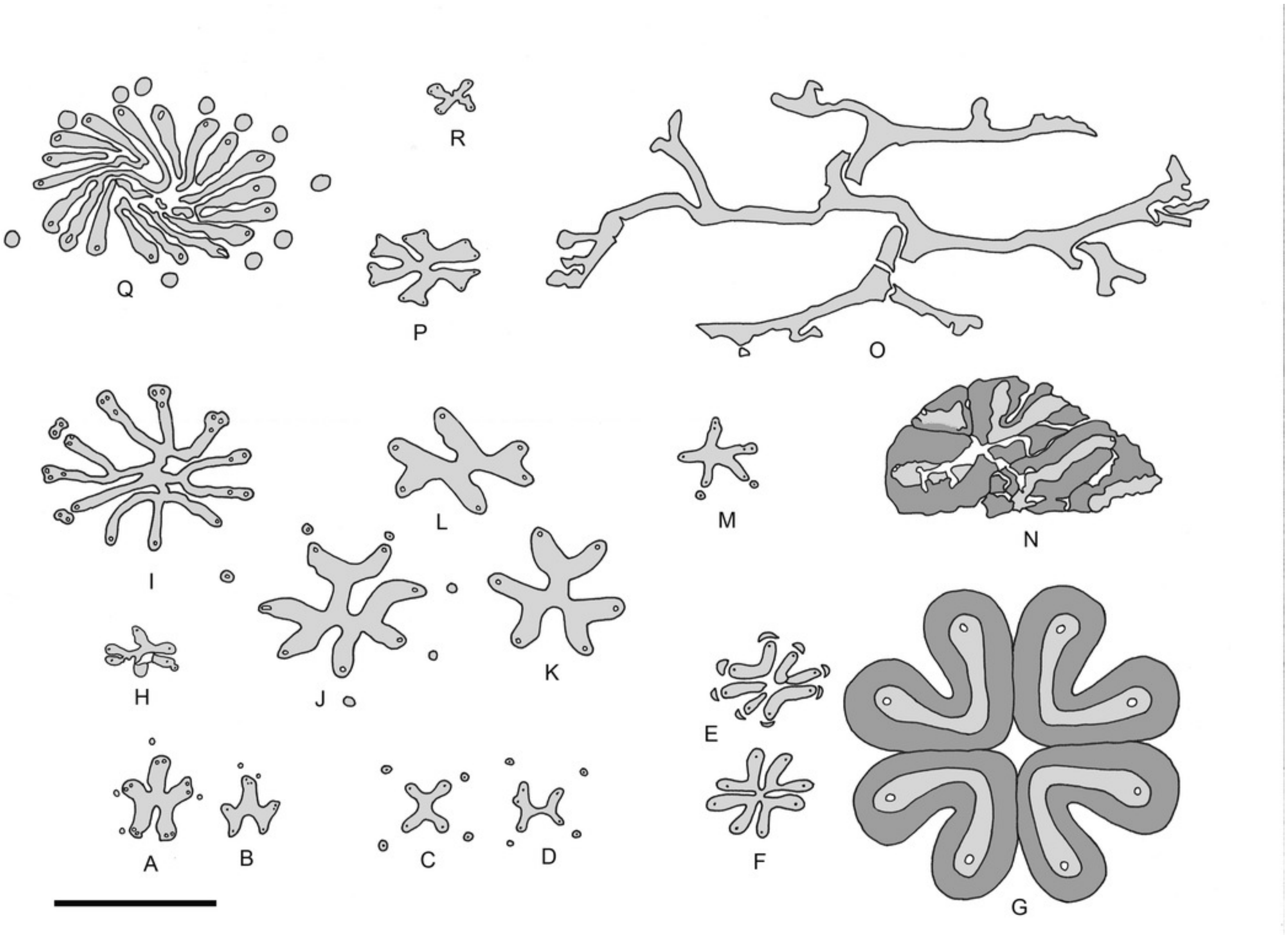

en
ic
oc
A
B
C
D

Figure 5

Vascular system of Iridopteridales and allies in transverse section; stratigraphically youngest taxa at top.

(A) - (B) *Iridopteris eriensis.* (C) - (D) *Arachnoxylon minor.* (E) - (G) *Metacladophyton tetraxylum.* (H) *Compsocradus laevigatus*. (I) *Asteropteris noveboracensis.* (J) - (L) *Arachnoxylon kopfii.* (M) *Ibyka amphikoma.* (N) *Metacladophyton ziguinum.* (O) *Keraphyton mawsonii.* (P) *Denglongia hubeiensis*. (Q) *Rotoxylon dawsonii*. (R) *Serripteris feistii*. Scale bar 5 mm. Secondary-type xylem in grey. (A) - (D), (I) - (M): adapted from Stein (1982); (E) - (G): adapted from Wang & Geng (1997); (H): adapted from Berry & Stein (2000); (N): adapted from Wang & Lin (2007); (P): adapted from Xue, Hao & Basinger (2010); (Q): adapted from Cordi & Stein (2005); (R): adapted from Rowe & Galtier (1989).


Q
R
P
O
I
L
M
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