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Abstract

For Devonian palaeobotany, Australia represents one of the most geologically well-documented areas of the understudied Gondwana palaeocontinent. Despite this asset, the Australian plant record is still insufficiently known for this period. This situation is detrimental to a satisfactory understanding of the evolution and diversification patterns of vascular plants at a crucial moment in Earth's history, when they acquired modern attributes and when the main extant lineages originated.

This paper documents a plant assemblage from a locality near the town of Gooloogong in central New South Wales, based on fossils collected by A. Ritchie and R. Jones of the Australian Museum, Sydney, in 1973. Additional material was collected in 2004 by our team. Fossils are preserved in the form of casts, adpressions preserving external morphology, and permineralizations showing internal anatomy. The Lycopsida are represented by *Leptophloeum rhombicum*, the Cladoxylopsida by *Denglongia* cf. *hubeiensis*, and the Progymnospermopsida by various organs attributed to the Archaeopteridales, i.e. a root of *Callixylon* sp., branches of *Archaeopteris* sp., and a leaf of *Archaeopteris macilenta*.

This association, which is typical of the Frasnian of South China supports a Frasnian age for the Gooloogong plant assemblage. It also confirms the existence of floristic exchanges between the northeastern part of Gondwana and South China at this time, and supports a trend towards the homogeneization of floras during the Late Devonian.

Keywords: Plant assemblage; Gondwana; Frasnian; Lycopsida; Archaeopteridales; Cladoxylopsida.

1. Introduction

Recent studies of Silurian-Devonian plant diversity have addressed the issue of sampling evenness in the fossil record, and how this problem can distort our understanding of the patterns of evolution, diversification and dispersal of vascular plants during the early stages of terrestrialisation (Capel et al., 2022; Liu et al., 2024). This period is indeed crucial in the history of land plants, which evolved specialized tissues and organs leading to a diversity of morphologies, growth forms and reproductive strategies adapted to a wider range of habitats, and fundamental to the construction of modern ecosystems (Kennedy et al., 2012; Cressler III et al., 2016; Friedman, 2017; Wang et al., 2019; Stein et al., 2020; Davies et al., 2024). Australia, in the northeastern part of Gondwana, is one of these zones with relatively little up-to-date information on plants of the Silurian-Devonian time range. Over the past 30 years, a number of studies have been carried out in both historical and new Australian localities. Plants from the Silurian-Early Devonian of Victoria (Mc Sweeney et al., 2020, 2021a, b, 2022 a, b), the Middle Devonian of Queensland (Meyer-Berthaud et al., 2003) and the Middle to Late Devonian of New South Wales

(Meyer-Berthaud et al., 2016, 2021; Champreux et al., 2020) have been described and their taxonomic affinities discussed in the light of recent advances in systematics. Yet, they remain few compared with discoveries made in the same time for South China (Wang et al., 2007; Hao and Xue, 2013; Xue et al., 2018). This sampling unevenness is particularly problematic for testing the level of floristic exchanges, as well as the palaeogeographic and palaeoclimatic proximity between these two areas, which are considered to constitute a single palaeogeographic unit in some diversity studies (Cascales-Miñana and Meyer-Berthaud, 2015; Capel et al., 2023; Liu et al., 2024). Further efforts are therefore needed to describe new Devonian plant assemblages in Australia.

In this context, we document here a small assemblage of plants from a locality near Gooloogong in central New South Wales. The first plant fossils were collected in 1973 from a newly constructed road cutting by A. Ritchie and R.K. Jones, and are lodged at the Australian Museum, Sydney (AMF.57162-164). The labels attached to these specimens indicate they were examined by Mary White, who identified in the material a new taxon '*Hostinella xylaster* White 1981'. However we were unable to find any published description of '*Hostinella xylaster'*. Neither the name nor the 1981 reference are recorded in the ledgers of the Australian Museum, and it was a practice of Dr White to indicate a manuscript name on specimens before she had published a description (Patrick Smith, *pers. comm*. July 23, 2024), so evidently her proposed taxonomic name is a *nomen nudum*.

The quality of preservation of the specimens motivated us to revisit the Gooloogong plant locality. In 2004 two of us (BMB & GCY), and Philippe Gerrienne from the University of Liège, organized a field trip there and collected additional samples. This paper describes the most informative specimens, including those first collected by Ritchie and Jones, and discusses their stratigraphic and palaeogeographic significance.

2. Geological setting

The locality is a road cutting ~6 km SW from the village of Gooloogong, on the Gooloogong-Grenfell Road, central NSW (loc. 1, Fig. 1). The most recent geological map (Grenfell 1:100,000 geological sheet, 1999) shows this as a basal 'Gooloogong Member' within the Hunter Formation, a widely outcropping fine-grained formation within the Upper Devonian Hervey Group (Fig. 1A). The road cutting is actually the type section for the Gooloogong Member of the Hunter Formation, formalised by Young et al. (2000) for the 'Gooloogong beds' of Colwell (1974, p. 28). Colwell (1974, fig. 13) recorded 96 m of exposure on the northern side of the road, but the lower 20 m of coarser reddish sediments was reassigned by Young et al. (2000) to the upper part of the underlying Peaks Formation. This left ~80 m of Colwell's section as the type section for the Gooloogong Member, comprising easterly dipping buff sandstones and siltstones, with minor components of red siltstone, shales and fine green sandstone. A new measured section presented below increases the thickness to ~116 m.

Colwell (1974) considered his 'Gooloogong beds' to lense out in both directions, but subsequent mapping (Young 1999a) indicated more extensive outcrop. This is a generally recessive unit with poor exposure, and the type section was only discovered when the road cutting was constructed in the early 1970s. Young (1999b, p. 145) recorded lingulid brachiopods and placoderm plates from these beds, suggesting correlation to the north across the Lachlan River with transitional beds between the Mandagery Formation ('Sandstone') and lower 'Pipe Formation' (renamed 'Mount Cole Formation' by Young et al. 2000). Contrary to previous correlations, the biostratigraphy of placoderm fish assemblages demonstrated that the Peaks Formation on the south side of the Lachlan River was the correlative across the river of the Mandagery Formation, the most prominent sandstone north of the river (Young 1999b). Across 3-5 km of non-outcrop on river flats of the Lachlan River, the first outcrops to the north from the Gooloogong road cutting (loc. 1, Fig. 1) is the Belubula River stratigraphic section, which includes the well-known Canowindra fossil fish assemblage near the top of the Mandagery Formation (loc. 2, Fig. 1). This was also interpreted as late Frasnian in age (Young, 1999b; Young, 2024). It was suggested that the change to fine-grained deposition up-section, representing the transition from the Peaks Formation to the Gooloogong Member at the fossil plant site, and the Mandagery Formation to the Mount Cole Formation at the fossil fish site, was the lithological manifestation of a marine flooding event causing brackish water conditions (with lingulid brachiopods in both sections), this event provisionally aligned with the late Frasnian maximum transgression of the Devonian sea level curve (e.g. Young and Turner, 2000; Young et al., 2010). The Frasnian age contradicts a recent interpretation based on other criteria, that the fossil fish at Canowindra and some other Hervey Group localities is younger, of Famennian age (Retallack 2024 ; see discussion in Young, 2024). The results reported here support a Frasnian age for both occurrences.

The new plant material from the Gooloogong Member type section described below was collected from both sides of the road (23 Nov 2004), these representing the same or a very similar horizon (GR 626999 6276297 north side; GR 626986 6276274 south side). To locate the plant horizon, a new section was measured using a tape (GCY) in the road gutter on the northern side (direction 75°E for first 50 m, then 65°E). The base of the measured section at the W end (GR 626922 62762747) was a ~40 cm thick cross-bedded sandstone with mud flakes (dip 50°E, strike 010), representing the approximate top of the underlying Peaks Formation. From this bed, placoderm plates (*Bothriolepis*, *Remigolepis*) were collected in 1994 (GCY locality 94/7). The following observations were made at horizons identified in our new measured section (stratigraphic thickness correction based on an assumed average dip of 45° east):

<u>30 m</u> (dip 43°E, strike 015): bed containing lingulid brachiopods.

<u>45 m</u>: beds with ripples.

<u>57 m</u> (dip 48°E, strike 015): plant bed (large axes) collected by P. Gerrienne.

<u>65 m</u>: palaeomagnetic drill holes (evidently locality 11 of Li et al. 1988)

<u>71 m</u>: return to red mudstone.

<u>79 m</u>: alternating pinkish/bluff siltstone/shale.

<u>81 m</u> (GR 627024 6276312): fallen sandstone blocks; approximate level for *Groenlandaspis* from GCY locality 96/57 (a tuberculate species; referred by Young et al. 2000, p. 134 to fossil fish Assemblage A of the Hunter Formation).

<u>93 m</u> (dip 40°E, strike 040): well bedded with faint parting lineations (similar current direction to ripples).

<u>116 m</u>: highest in situ outcrop on the north side of the road cutting.

3. Material and methods

AMF.57162 at the Australian Museum in Sydney is a siltstone slab, with its counterpart divided in two portions, separately numbered AMF.57163 and AMF.57164. These show several branching axes preserved in compression, and with different orientations (Fig. 2B, D; Fig. 3). Specimens that branch alternately (e.g. specimen 1 in Fig. 2B and Fig. 3A, C, D) show too few characters to be identifiable. Specimen 2, visible on slabs AMF.57162 and AMF.57164 (Fig. 2D, E; Fig. 3A, B), and specimen 3, visible only on slab AMF.57163 (Fig. 2B; Fig. 3C), are more complete and described in the next section. Specimen 3 is partly permineralized, and three thin-sections labelled AM.6968 were prepared from it, evidently by or for Mary White. A fourth thin-section, numbered AM.6973 is attributed to slab AMF.57164 on its label despite the fact that there is no anatomically preserved axis on that rock slab. The specimen from which this slide was made is therefore unknown. The thin-section is described in the following section, but is too incomplete to be assigned to a specific taxon (as noted above, Mary White's name '*Hostinella xylaster'* on the labels is a *nomen nudum*, and is thus not retained in this article).

Additional specimens collected from the locality in 2004 were relatively numerous but fragmentary, and distributed without any preferential orientation in the matrix. They represent vegetative organs preserved as casts, adpressions (i.e., impressions and coalified compressions) and limonitic permineralizations, the latter not as well preserved as the anatomically preserved axes in the Ritchie and Jones material. The new permineralized axes have been embedded in epoxy resin, sliced, and when necessary, treated with oxalic acid to enhance the contrast. Photographs were taken with a Keyence VHX-700 digital microscope. The specimens from 2004 described below are deposited at the Australian Museum in Sydney under numbers AMF.165612 to AMF.165616.

4. Systematic palaeobotany

Subdivision Lycophytina Kenrick and Crane, 1997
Class Lycopsida Kenrick and Crane, 1997
Order Isoetales Prantl, 1874
Family Leptophloaceae Kräusel and Weyland, 1949
Genus *Leptophloeum* Dawson, 1862 emend. Li et al. 1986

Leptophloeum rhombicum Dawson, 1862

Material studied: Specimen AMF.165612, Australian Museum, Sydney; cast and mould.

Description: A single type of lycopsid has been collected at the fossil site during our 2004 field trip. The specimen illustrated on Fig. 2A consists of the inner cast and the mould of a 5 cm wide axis. The cast surface is covered with closely spaced impressions of leaf cushions. They are rhombic and tangentially elongated, averaging 3-4 mm in height and 8 mm in width. Leaf scars are not visible.

Remarks: Specimen AMF.165612 represents a *Leptophloeum* axis. *Leptophloeum* Dawson is a member of the Isoetales (Geng, 1990). Two species are currently recognized in this genus, the type-species *L. rhombicum* Dawson first described in Maine, eastern USA (Dawson, 1862), and *L. australe* (Mc Coy) Walton (1926) originally described in Australia. However, many authors consider that *L. australe* is conspecific with *L. rhombicum*, which has priority (Carruthers, 1872; Walton, 1926; Sze, 1952; Li et al., 1986; Wang et al., 2005; Prestianni and Gess, 2014). Both species show a unique type of peltate sporophylls. The attribution of fossil remains to one or other of these species is based mainly on their geographical origin. The characteristics that could distinguish them, such as the rhombic versus hexagonal shape of the leaf cushions, the degree of tangential elongation of these cushions, or the central versus apical position of the leaf scars, can be found in both morphospecies and have no real taxonomic significance.

Leptophloeum axes from Kazakhstan have been reported to measure up to 20 cm in diameter (Lemoigne, 1982), some Australian specimens 30-40 cm, and the largest trunk from China, more than 50 cm (references in Wang et al., 2005). However, these large specimens have never been illustrated, which casts doubt on the validity of these claims. The 5 cm wide specimen from Gooloogong compares in external dimensions with axes from the Upper Devonian of Majors Creek NSW (Dunstone & Young 2019, fig. 2a-b), and another from a nearby locality across the Lachlan River figured by Retallack (2024, fig. 4a; scale incorrect, 5-6 cm across). An 8 cm wide Frasnian axis of a *L. rhombicum* specimen from Hubei was used by Wang et al. (2005) to reconstruct the plant as a small tree bearing ephemeral lateral branches. The Gooloogong specimen is also comparable in size to the stem at root junction of the Famennian specimens from South Africa reported with a cormose rhizomorph (Prestianni and Gess, 2014). However, its leaf cushions are smaller, those of the Chinese and South African specimens measuring up to 10 mm in height and 12 mm in width. The Gooloogong specimen could therefore represent the distal part of the trunk of a larger tree than the last two mentioned.

Subdivision Euphyllophytina Kenrick and Crane, 1997
Class Cladoxylopsida Pichi-Sermolli, 1959

Order and Family Incertae sedis
Genus *Denglongia* Xue and Hao, 2008 emend. Xue, Hao and Basinger, 2010

Denglongia cf. hubeiensis

Material studied: Specimen 3 on rock slab AMF.57163 and three thin-sections, two transverse and one longitudinal, all labelled AM.6968, Ritchie & Jones collection, Australian Museum, Sydney; partly permineralized specimen.

Description: Specimen 3 dips obliquely in the matrix of rock slab AMF.57163 (Fig. 2B; Fig. 3C, D). It is preserved at the level of a node on the upper surface, where it is partly hidden by specimen 1. Three branches with up to 4.4 mm broad swollen bases are visible, two branches in front view, and a third one partly folded (Fig. 2C). It is likely that four or more branches should have coexisted at this node. The central part of the axis is anatomically preserved. It is 3.1 x 3.4 mm wide on the upper surface of the rock slab (Fig. 2C). The two available transverse sections correspond to the lower surface where the outline of the anatomically preserved part is fluted (Fig. 2F). They show a portion of the vascular cylinder, which is made of primary xylem only (Fig. 4A; Fig. 5A). It consists of two main ribs connected at their inner ends. The largest rib is 1.5 mm long radially, 350 µm wide at base, enlarging to 820 µm at its outer end. Rib tips are slightly invaginated, forming two shallow lobes (Fig. 4A). Tracheids measure 25-95 µm in diameter. The smallest ones, comprising the protoxylem strands, are concentrated in the distal lobes and are not associated with parenchyma cells or cavities (Fig. 4B). Whether protoxylem maturation is mesarch or exarch is uncertain. In longitudinal section, tracheids show scalariform thickenings (Fig. 4C). The few thin-walled, narrow and elongated cells bordering the xylem may represent the phloem. The inner cortical cells are deformed (IC in Fig. 4A). The preserved ones are 35-85 µm wide in transverse section and up to 115 µm high.

Remarks: With its whorled organotaxis, deeply lobed primary vascular system, and lack of secondary xylem, specimen 3 is close to the Iridopteridales, the transitional cladoxylopsids and some cladoxylalean cladoxylopsids that are all part of the cladoxylopsids *sensu lato* (Durieux et al., 2021; Chu et al., 2024). The stele of specimen 3 in the available transverse sections is incomplete but it shows iridopterid characters such as an actinostelic organization with several lobes connected at their inner ends, largest tracheids located in the center of the ribs, and protoxylem strands at rib tips. In the iridopterids, however, the protoxylem strands are clearly mesarch and generally associated with a lacuna (Fig. 5E, G). All show xylem ribs with sides that are parallel, not enlarged outwards like those of specimen 3.

Among the cladoxylalean cladoxylopsids, *Metacladophyton tetraxylum* from the Givetian of Hubei has 3.5-7 mm wide stems with first-order branches borne in whorls, comparable in size and organization to specimen 3 (Wang and Geng, 1997). However, the steles of *M. tetraxylum* stems have ribs with parallel sides, which do not form pairs of lobes distally (Fig. 5D). In addition, protoxylem strands are clearly mesarch and associated with lacunae at branching level. In the same informal group, the Famennian cladoxylopsid *Polyxylon australe* from Queensland also shows branches borne in whorls (Meyer-Berthaud et al., 2007). Its stems have stelar ribs connected proximally and forming pairs of lobes distally like in specimen 3 (Fig. 5F). Protoxylem strands occur at the very tip of the lobes and are described as exarch. However, the stems of *P. australe* are much larger, with up to 10 branches per whorl. Specimen 3 does not either correspond to a branch of *P. australe*. Indeed, the vascular supplies of branches in the latter taxon bear no resemblance to the vascular system of specimen 3. They are bilaterally symmetrical, with separate xylem strands.

The fossils whose anatomy most closely resembles that of specimen 3 are the main axes of *Denglongia*, a monospecific genus of Frasnian age from Hubei presented as a transitional cladoxylopsid (Xue and Hao, 2008; Xue et al., 2010). The type species *D. hubeiensis* has been entirely reconstructed. The plant consists of a main axis, and two orders of branches arranged in whorls and bearing ultimate appendages (Xue and Hao, 2008). Main axes are comparable in diameter to specimen 3 and have 4-6 branches at the nodes, which corresponds to the number of branches also expected for specimen 3 if it was complete. Their actinostele has five to six ribs, each bifurcating into two shallow lobes distally (Xue et al., 2010) (Fig. 5B, C). Despite these similarities, we hesitate to attribute specimen 3 with certainty to the species *Denglongia hubeiensis* for two reasons : (i) protoxylem strands are described as mesarch in the Chinese taxon; (ii) the architecture of the Australian plant is only partially known. Therefore, in this paper specimen 3 is designated as *Denglongia* cf. *hubeiensis*.

Subdivision Euphyllophytina Kenrick and Crane, 1997
Class Progymnospermopsida Beck, 1960
Order Archaeopteridales Zimmermann, 1930
Family Archaeopteridaceae Schmalhausen, 1894
Genus *Archaeopteris* Dawson, 1871 emend. Stur, 1875

Archaeopteris macilenta Lesquereux, 1884

Material studied: Specimen AMF.165613, Australian Museum, Sydney; adpression.

Description: A small laminated leaf with a missing base is preserved as an adpression (Fig. 2I; Fig. 6A). It measures 8.4 mm long, 2.8 mm wide proximally, and about 4.8 mm distally. Its margins are slightly concave. The leaf shows a rounded apex dissected into ten shallow lobes, the widest ones dividing again at the very tip. Individual lobes are 300-440 µm wide and 1300-1640 µm long. A faint cellular pattern is present on the leaf surface. Veins are not visible. Another laminated structure is partially visible on the same slab (arrow on Fig. 6A). It is very close to the first, has the same orientation, and divides into lobes at the same level. It may be a neighboring leaf borne on the same axis and not overlapping the first one. Another possibility is that the two structures are parts of a single leaf showing a very deep initial division of the lamina.

Remarks: Specimen AMF.165613 is identified as a sterile leaf of *Archaeopteris macilenta*. *Archaeopteris* is a progymnosperm genus based on the leafy branches of trees extending from the mid-Givetian to the latest Famennian, possibly to the earliest Mississippian (Fairon-Demaret et al., 2001; Decombeix et al., 2011; Wang, 2011; Stein et al., 2020). It has been known for 150 years and many species have been described, but in the 1970s, revisions of *Archaeopteris* reduced the number of species to six (Phillips et al., 1972). Only one recognized taxonomic addition from South Africa has been made since then (Anderson et al., 1995). At present, four species of *Archaeopteris* are reported with dissected sterile leaves : *A. fissilis* (Schmalhausen, 1894; Nathorst, 1904), *A. sphenophyllifolia* (Lesquereux, 1884), *A. notosaria* (Anderson, 1995), and *A. macilenta* (Lesquereux, 1884; Carluccio et al., 1966) from the NE USA, Europe (Belgium, Ireland), Bear Island, North Timan, South China (Lesquereux, 1884; Arnold, 1936, 1939; Cai, 1981; Cai and Wang, 1995; Orlova et al., 2016). Comparing sterile leaves at the same scale of *A. sphenophyllifolia*, *A. notosaria, A. fissilis* and *A. macilenta* with the Gooloogong example shows that those of *A. sphenophyllifolia*, *A. notosaria* and *A. fissilis* are more deeply dissected (Fig. 6A, C, D, E). Unlike the latter, those of *A. fissilis* have long and very narrow segments whereas leaves of *A. sphenophyllifolia* and *A. notosaria* have much larger dimensions and broader lobes. The Gooloogong leaf is comparable to those of *A. macilenta* in overall shape, size, and depth of lamina incision (Fig. 6A, B). Its veins are hardly visible, a trait also mentioned for *A. macilenta* (Lesquereux, 1884; Arnold, 1936).

Archaeopteris sp.

Material studied: Specimens AMF.165614 and AMF.165615 and corresponding thin-sections, Australian Museum, Sydney; permineralizations.

Description: Several anatomically preserved axes measuring less than 7 mm wide were collected during the 2004 field trip. They are all entirely decorticated. The two best-preserved specimens are AMF.165614, which is 3.7 mm wide in its largest dimension (Fig. 4D; Fig. 7A), and AMF.165615, which is 2.6 mm wide (Fig. 4E; Fig. 7B).

The vascular systems of AMF.165614 (Fig. 4D, G) and AMF.165615 (Fig. 4E) are partially preserved and somewhat flattened. They consist of a lobate siphonostele surrounded by a relatively narrow cylinder of dense wood. The stele in specimen AMF.165614 shows four, possibly five lobes (Fig. 7A); that of AMF.165615, six lobes (Fig. 7B). The stele center in specimen AMF.165614 consists of a badly preserved parenchymatous tissue (Fig. 4D). There is no evidence of isolated tracheids or strands of sclerotic cells scattered in this tissue. Pith cells measure 40-70 µm wide. The primary xylem tracheids in the lobes measure 30-50 µm in diameter. In both specimens, each lobe shows one, or 2-3 radially aligned mesarch protoxylem strands (Fig. 4G; Fig. 7A, B). The surrounding wood in AMF.165614 is up to 560 µm thick, that of AMF.165615, 480 µm. In both specimens, secondary xylem tracheids are 15-40 µm wide tangentially and 20-60 µm wide radially. Rays are uniseriate and 10-19 µm in width.

Remarks: Specimens AMF.165614 and AMF.165615 are interpreted as penultimate branches of *Archaeopteris sp.* Carluccio et al. (1966) demonstrated that the so-called fronds of *Archaeopteris* were not compound leaves but the distal branched systems bearing simple leaves of *Archaeopteris* trees. Their assessment was based on the analysis of anatomically preserved « fronds » of *Archaeopteris macilenta* collected in lower Frasnian localities of New York. Later, Kenrick and Fairon-Demaret (1991) showed that, despite differences in their leaf morphology, the penultimate and ultimate axes of Famennian specimens of *A. roemeriana* (= *A. halliana*) from Belgium had the same anatomy as those of *A. macilenta*. The vascular anatomy of the other species of *Archaeopteris* is unknown, but they likely shared the same general organization.

The primary vascular system in the penultimate axes of *A. macilenta* and *A. roemeriana* (= *A. halliana*) comprises a central pith and, depending on the level, is eustelic to siphonostelic. It is lobate and shows up to ten ribs, each with two mesarch protoxylem strands connected by small radially elongated cells (Fig. 7D). Secondary xylem may be present, and is thicker in the basal parts of the penultimate axes. Secondary xylem is absent in ultimate axes. The primary vascular system of fertile ultimate axes is comparable in the two species and shows up to seven ribs (Fig. 7E). That of the vegetative ultimate axes of *A. roemeriana* (= *A. halliana*) shows an abaxial-adaxial differentiation and may lack a pith at some levels. In *Actinopodium*, the probable branches of the *Archeopteris*-type plant *Svalbardia* from the Frasnian of Spitzbergen, and in *Siderella*, a genus representing branches of a late Famennian-Tournaisian archaeopterid, additional mesarch protoxylem strands occur between the stelar lobes (Read, 1936; Høeg, 1942; Carluccio et al., 1966; Piepjohn and Dallmann, 2014).

Specimens AMF.165614 and AMF.165615 possess some secondary xylem and do not show any protoxylem strands between the lobes of their steles. They represent penultimate branches of *Archaeopteris*. The specific identity of these specimens is uncertain and cannot currently be resolved based on vascular characters only. Therefore, we refer to them as *Archaeopteris sp*.

Genus *Callixylon* Zalessky, 1911
Callixylon sp.

Material studied: Specimen AMF.165616, Australian Museum, Sydney and corresponding thin-sections; permineralization.

Description: AMF.165616 is 5.2 mm wide and entirely decorticated (Fig. 4F; Fig. 7C). Its stele is massive and made of primary xylem tracheids only (Fig. 4I). It shows an angular contour whose limits are uneasy to determine. Protoxylem strands are inconspicuous and certainly not mesarch as in the preceding specimens. Primary xylem tracheids are 30-95 µm wide. The surrounding wood is up to 2.2 mm broad and thicker than that of AMF.165614 and AMF.165615. It does not show any growth ring. Secondary xylem tracheids are 25-60 µm wide tangentially and 30-80 µm wide radially. Rays are uniseriate and 13-25 µm wide (Fig. 4H). They seem made of parenchyma cells only but preservation is such that the presence of rare ray tracheids may be unnoticeable.

Remarks: With its angular protostele, its inconspicuous protoxylem strands and abundant secondary xylem, AMF.165616 is interpreted as an *Archaeopteris* root. It is assigned to *Callixylon* since anatomically preserved axes other than the distalmost axes of *Archaeopteris* are referred to this genus.

Its wood is characterized by narrow rays like most other archeopterid roots described thus far. Its protostele, however, looks different from the four-lobed protosteles of many roots from New York, the Canadian Arctic, and Donbass, among them those assigned to the root species *Callixylon petryi* (Beck, 1953; Andrews et al., 1965; Snigirevskaya, 1984) (Fig. 7F). It is also different from the pentagonal stele of a root from Morocco (Meyer-Berthaud et al., 2013) and the triradiate stele of *Callixylon seamrogia* from Ireland (Durieux et al., 2025). As for specimens AMF.165614 and AMF.165615 described above, the specific identity of AMF.165616 is uncertain, therefore it is assigned to *Callixylon sp*.

Family Incertae sedis
Genus Incertae sedis
Gen. et sp. Indet. 1

Material studied: Specimen 2 on rock slab AMF.57162, Australian Museum, Sydney; adpression.

Description: Specimen 2 on AMF.57162 is a 18 mm-long portion of stem broken off at a node showing a pair of opposite first-order branches (Fig. 2D; Fig. 3A). There are no depressions, scars or marks at this node to indicate the production of additional branches or appendages. The stem is 3.1 mm wide and shows longitudinal striations that are clearly visible on the counterpart, AMF.57164 (Fig.2E, H). These striae may represent the outer surface of the vascularization, which was fluted or made up of separate strands. Small projections are present below the node, but not elsewhere on the stem (Fig. 2E, G). Their nature is uncertain but they could correspond to spines. Both first-order branches have swollen bases. They do not show any spines or branched appendages attached basally or more distally. The best and longest-preserved branch, on the right in Fig. 2D and Fig. 3A, measures about 1.6 mm wide and 60 mm long up to a point where it divides into two small opposite second-order branches lying obliquely relatively to the rest of the specimen. Again, there are no marks at this node to indicate that further second-order branches have been produced.

Remarks: The stem of specimen 2 and its opposite branches show long internodes that are not covered with spines and do not show the production of ultimate appendages. Branches are borne at wide angles. This morphology has certain similarities with that of some iridopterids and allies known to date in the Cladoxylopsida *sensu lato*, but it doesn't correspond exactly to any of them.

Stems and branches in the iridopterid genus *Compsocradus* lack spines but they are covered with densely arranged ultimate appendages (Berry and Stein, 2000; Fu et al., 2011). Branches are not opposite but may rather look alternate. They form a more acute angle with their supporting axis than in the Goologong specimen. Axes of *Denglongia hubeiensis* are not spiny, and show long internodes (i.e., long distance between the successive levels of branches), but branches are borne in whorls rather than oppositely (Xue and Hao, 2008). Furthermore, first-order branches produce ultimate appendages proximally, below the whorls of second-order branches.

In *Metacladophyton tetraxylum,* the distance between branches is relatively long and second-order branches are produced oppositely; ultimate appendages are borne on the second-order branches, rarely on the first-order ones (Wang and Geng, 1997). However, a main difference with the Gooloogong specimen is that the first-order branches are not opposite, but borne in whorls. In addition, and whereas Wang and Geng (1997) described the axes of *M. tetraxylum* as naked, Wang and Lin (2007) argued that all axes in the genus *Metacladophyton*, including those of *M. tetraxylum*, were spiny.

Specimen 2, with its two orders of opposite branches, is reminiscent of certain aneurophytales, a group of Progymnospermopsida that flourished during the Middle and early Late Devonian. The genus *Tetraxylopteris*, initially described from Frasnian localities of New York state, is characterized by stems bearing several orders of opposite and decussate branches (Beck, 1957). It comprises two species, one of which (*T. reposana*) reported from Venezuela (Hammond and Berry, 2005). Another species, as yet unnamed, has been reported from the Givetian-Frasnian locality of Bunga Pinch Quarry in southern New South Wales (Meyer-Berthaud et al., 2016). The Gooloogong specimen differs from these *Tetraxylopteris* species by its more slender axes. More importantly, its branches have no organs, either branches or ultimate appendages, attached to their very base, as is the case in *Tetraxylopteris*.

Specimen 2 does not correspond to any known taxon. It shares morphological characters with members of both the Cladoxylopsida *sensu lato* and the Aneurophytales. Further anatomical data are required to determine its affinities.

Gen. et sp. Indet. 2

Material studied: : Specimen AMF.6973, one transverse thin-section, Australian Museum, Sydney; anatomically preserved axis.

Description: Specimen AMF.6973 is entirely decorticated and represented by a single transverse section showing two parts of a small, incomplete, solid xylem ring surrounding an empty central zone (Fig. 4J). The specimen has been compressed and the original shape of the central zone, whether oval, circular or more complex, is open to question. Its right side on Fig. 4J has been moved down the slide. When repositioned, the specimen measures 2.2 x 0.8 mm wide and the empty central zone 1.5 x 0.4 mm. The xylem is up to 550 µm thick. Tracheids are organized in radial files, with new rows intercalated in places (Fig. 4K, L). Tracheids are narrow, mostly rectangular, measuring 10-18 µm tangentially and 16-27 µm radially. The presence of rays is doubtful. If present, they would be rare, inconspicuous, and their cells would have had about the same radial dimension as the neighboring tracheids. With or without rays, this tissue is organized as a secondary xylem (= wood). Its inner border is smooth and regular, indicating that the limit with the primary vascular system, which occupied the central zone, was clear, without any interpenetrating elements (Fig. 4K, L). Two, possibly three, irregularly shaped areas of tracheids on the inner surface of the wood may correspond to vascular traces to appendages, but again, these may also be compression artifacts.

Remarks: Specimen AMF. 6973 corresponds to the vascular part of a small axis in transverse section. It is characterized by (i) its solid secondary xylem ring with inconspicuous rays if any, (ii) narrow and mostly rectangular secondary tracheids, and (iii) a clear, smooth limit between the secondary xylem and the primary vascular system, which is not preserved. The lack of longitudinal section prevents from checking the actual presence of rays in the wood, and from characterizing the type of pitting on tracheid walls. At present, we do not know any Middle to Late Devonian lycopsids, cladoxylopsids or progymnosperms that share such a set of characters.

Several woody lycopsids of this time-range (e.g. *Longostachys*, *Leptophloeum*, *Lobodendron*, *Sublepidodendron*) have a primary vascular cylinder with a smooth contour, which is distinct from the surrounding wood (Cai and Qin, 1986; Cai and Chen, 1996; Wang et al., 2002; Wang and Xu, 2005; Liu et al., 2015). Among them, the Famennian genus *Lobodendron* is represented by small axes characterized by secondary tracheids described as square to rectangular, and with a diameter comparable to that of the Gooloogong specimen (Liu et al., 2015). However, unlike the latter, all these lycopsid genera have a secondary xylem dissected in sectors or crossed by wide rays generally associated with leaf traces.

Numerous cladoxylopsids (e.g. *Xenocladia*, *Metacladophyton*, *Polypetalophyton*, *Shougangia*, *Xinhangia*) or fern-like genera such as *Rhacophyton* possess elongate vascular strands that could compare with the Gooloogong specimen (Arnold, 1952; Andrews and Phillips, 1968; Matten, 1974; Lemoigne and Iurina, 1983; Wang and Geng, 1997; Hilton et al., 2003; Wang and Lin, 2007; Wang et al., 2018; Yang and Wang, 2022). In addition, rays are described as absent in the wood of *Xenocladia* (Lemoigne and Iurina, 1983). However, none of these taxa shows an inner limit of the secondary xylem as sharp as that of the Australian specimen and their secondary tracheids are all much larger in diameter.

The secondary xylem in the aneurophytalean and archaeopteridalean progymnosperms possess visible rays and their tracheids are also larger in diameter than those of the Gooloogong specimen (Dannenhoffer and Bonamo, 2003, and references therein). It is thus not possible to assign this isolated fragment of wood to a known taxon.

5. Discussion

The Gooloogong plant assemblage encompasses specimens preserved as adpressions, which provide information on their external morphology, and specimens preserved as permineralizations, which provide information on their internal anatomy. The Gooloogong assemblage includes representatives of the three major lineages that flourished from the Middle to the Late Devonian, the Lycopsida with *Leptophloeum*, the Cladoxylopsida *sensu lato* with *Denglongia*, and the Progymnospermopsida with *Archaeopteris* and *Callixylon*.

Leptophloeum is known worldwide, and its stratigraphic extension spans the entire Late Devonian, and the Mississippian. It has been observed in localities of N. America, Spitzbergen, Siberia, Kazakhstan, China, Japan, Australia, Libya, Egypt and South Africa (Sze, 1952; Plumstead, 1967; Lemoigne, 1982; Li et al., 1986; Wang et al., 2005; Prestianni and Gess, 2014; Xue et al., 2018; Dunstone and Young, 2019; Liu et al., 2024; El-Saadawi et al., 2025).

Archaeopterids, represented by leafy branch adpressions of *Archaeopteris* and related genera, as well as anatomically preserved stems and roots assigned to the genus *Callixylon*, range from the Givetian to the latest Famennian, perhaps to the earliest Mississippian. Their palaeogeographic distribution is also worldwide (Capel et al. 2023; Liu et al. 2024). The first records of archaeopterids in Australia were the brief descriptions of *Archaeopteris howitti* Mc Coy from Iguana Creek (Victoria; McCoy, 1876), and then from Genoa River on the New South Wales border (Dun, 1897; loc. 3, Fig. 1). Genoa River (Combyingbar Fm) is interpreted as Frasnian (Gould, 1975; Young, 2007), although the associated plant remains are reminiscent of Famennian associations in North America and Belgium (Meyer-Berthaud et al., 2016). The leaves of *A. howitti* have an entire margin (White, 1986) and appear similar to those of *A. halliana*, a species well represented in the northeastern United States, Quebec, Europe and Russia.

Although modest, the leaf described in this paper represents the first clear evidence for the presence of *A. macilenta* in Australia. Adpressed specimens of *A. macilenta* have been reported from a large number of localities worldwide, in the northeastern USA, Europe, Bear Island, North

Timan and South China (Lesquereux, 1884; Arnold, 1936, 1939; Cai, 1981; Cai and Wang, 1995; Guo and Wang, 2011; Orlova et al., 2016). *Archaeopteris macilenta* is particularly abundant in north American deposits of Frasnian age (Phillips et al., 1972). Along with *Leptophloeum rhombicum*, it is one of the most representative elements of the Frasnian plant assemblages of South China (Guo and Wang, 2011), precisely designated as the 'early Late Devonian *Leptophloeum rhombicum - Archaeopteris macilenta* floral assemblage' by Cai and Wang (1995).

Plant remains attributed to *Archaeopteris* sp. have previously been recorded from elsewhere in the Hervey Group. A fine-grained green sandstone block with a 35 cm long penultimate and ultimate branching system referred to *Archaeopteris* sp. was found in 1982 in a road cutting at Bindogundra 11 km east of Parkes (ANU 49399, in the collection of the Research School of Earth Sciences, ANU). A smaller similar block from the same site is held in the Australian Museum (AMF. ???). In April 2003, two of us (BMB and GCY) re-visited this site, at the northern extremity of Hervey Group outcrop in the Parkes Syncline (loc. 4, Fig. 1A), but no significant plant remains were found. However we collected more plant remains from another road cutting at ('The Dungeons') within the Bumberry Syncline (loc. 5, Fig. 1A), including *Leptophloeum* and a leaf of *Archaeopteris* sp. (AMF. ???). Both localities represent a similar stratigraphic level to the Gooloogong plant locality; i.e. transitional beds between the upper sandstones of the Mandagery Formation, and the overlying fine-grained Mount Cole Formation. Finally *Archaeopteris macilenta* has recently been claimed to occur in the Canowindra fossil fish assemblage (Retallack, 2024). This locality (loc. 2, Fig. 1) is situated 19 km NE of the Gooloogong plant locality across the Lachlan River. However, the published illustrations (Retallack, 2024, fig. 4b-c) are unconvincing, and according to Robert Jones and Patrick Smith (pers. comm. 2 April 2024) the illustrated specimens are not fossils, whilst the published registration numbers actually apply to fossil fish specimens from the Canowindra site. We therefore discount this occurrence.

The presence of *Denglongia* at Gooloogong is the first evidence for the existence of this genus outside southern China. It is further evidence in favour of a Frasnian age for the Gooloogong assemblage. *Denglongia* shares many characters with the Iridopteridales, such as a whorled arrangement of its branches and a stellate stele with protoxylem strands located at rib tips only. However, this genus differs from the iridopterids by its complex fertile organs and the lack of appendages inserted at the same nodes as branches. *Denglongia* was considered as a Cladoxylopsida incertae sedis by Xue et al. (2010). In Durieux et al.'s (2021) phylogeny where the cladoxylopsids *sensu lato* include the Iridopteridales and the cladoxylopsids *sensu stricto*, *Denglongia* was resolved as a transitional cladoxylopsid, in a basal position within the cladoxylopsids *s.s.*

Few cladoxylopsids have been reported from Australia, and *Denglongia* increases this number. The block of chert containing the specimens referred to as *Schizopodium davidi* by Harris (1929) and renamed *Astralocaulis davidii* by Hueber (1971) is suspected to represent a portion of the root mantle of an erect cladoxylopsid stem (Soria and Meyer-Berthaud, 2004). The block is believed to come from the Burdekin beds of Middle Devonian age in the Burdekin basin, Queensland (loc. 6, Fig. 1). All the other cladoxylopsids described to date have been collected in the Famennian locality of Barraba in New South Wales (Chambers and Regan, 1986; Meyer-Berthaud, 2021; loc. 7, Fig. 1). There, they are relatively diverse, consisting of *Polyxylon australe*, two species of *Cladoxylon* and a *Hierogramma* for the cladoxylopsids s.s. A fifth genus, *Keraphyton*, was assigned to the Iridopteridales, but this taxon shows a more complex stele than in any other iridopterid described thus far. As paleobotanical studies progress, it seems that cladoxylopsids, long ignored in this part of Gondwana, may have represented non negligible elements of the Australian flora between the Middle Devonian and the end of the Late Devonian.

The plant assemblage at Bunga Pinch Quarry in southern New South Wales (loc. 8, Fig. 1) is either Givetian or early Frasnian, a little older than the one at Gooloogong. The lycopsids of Bunga Pinch Quarry do not include *Leptophloeum*, the lycopsid trees of this locality being represented by specimens of the *Lepidosigillaria*-type (Meyer-Berthaud et al., 2016; Dunstone and Young, 2019). Most of the plant remains correspond to leafless axes up to 20 mm wide, with alternate or opposite branches. They look woody, suggesting progymnosperm affinities. Specimens characterised by opposite branches have been assigned to the aneurophytalean genus *Tetraxylopteris*, but we suspect that those with alternate branches also belonged to the Aneurophytales. Archeopteridalean progymnosperms and cladoxylopsids are absent at Bunga Pinch Quarry. The plant assemblages of Bunga Pinch Quarry and Gooloogong are therefore clearly different in composition. Given the current state of knowledge on Australian floras, it is premature to determine how age, environment or taphonomical conditions have contributed to this difference.

The paleogeographic affinities of Australian floras have changed during the course of the Devonian according to Capel et al. (2023). These authors noted weak differences between the floras of the Early Devonian (Pragian-Emsian), with Australia's flora closer to that of South China than to any other. These similarities had already been reported by Hao and Xue (2013) and McSweeney et al. (2021a). Middle Devonian floras, on the other hand, showed significant palaeogeographic differentiation. At this time, the Australian flora would have had more affinities with the Gondwanan flora than with the South China flora. Again according to Capel et al. (2023), this paleogeographic differentiation was reduced in the Late Devonian, with only two major latitudinal groups, an "Equatorial to mid-latitudes" phytochorion to which southern China was attached, and a "South Laurussia-Gondwana" phytochorion to which Australia was attached. The Late Devonian flora of Australia is far from being as well documented as that of other, more northerly, regions of the world, and its proposed affinities are likely to evolve with further investigations. The presence of *Denglongia* at Gooloogong suggests that the Late Devonian flora of Australia may have been closer to the contemporaneous flora of South China than hitherto estimated. In any case, this presence supports a trend towards a global homogenization of floras at the end of the Devonian. Similar affinities between eastern Australia and China in Devonian fish assemblages are summarised by Young and Lu (2020).

In the current stage of knowledge, the Gooloogong plant assemblage is not taxomically diverse. However, some specimens, too incomplete to be identifiable, are clearly distinct from the taxa recognized in this paper (*Leptophloeum*, *Denglongia, Archaeopteris*, *Callixylon*), indicating that this diversity is certainly underestimated. A special collecting effort is needed to gain a better appreciation of the plants that have colonized the Gooloogong area in the Late Devonian.

6. Conclusion

A new plant assemblage is documented in the Hervey Group, in central New South Wales, Australia.

- Gooloogong is the second New South Wales locality, after Bunga Pinch Quarry, to provide details on plants within the Givetian-Frasnian time interval. The Gooloogong plant assemblage is the youngest, and currently, shares no taxa with that of Bunga Pinch Quarry.
- The Gooloogong plant assemblage contains one of the oldest cladoxylopsids from Australia, and the first record of the genus *Denglongia* outside China. *Denglongia* is no longer an endemic genus of the Frasnian of South China.
- The Gooloogong plant assemblage provides the first direct evidence of *Archaeopteris macilenta* in Australia, where two species of *Archaeopteris* are now attested: *A. macilenta* with dissected sterile leaves from the Frasnian, and *A. howitti* (*A. halliana*?) with entire leaf margins, possibly from the Famennian.
- The *Leptophloeum rhombicum- Archaeopteris macilenta* association is representative of Frasnian-age plant assemblages in South China. The genus *Denglongia*, previously restricted to China, is also Frasnian. The association of *Leptophloeum rhombicum, Archaeopteris macilenta* and *Denglongia* at Gooloogong supports a Frasnian age for the locality. It also confirms floristic exchanges between Australia and South China at this time.

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Figure legends

Fig. 1. Geological setting for the fossil plant remains described in this paper. (A) outcrop pattern (black) for the Upper Devonian Hervey Group across the Bathurst and Forbes 1:250,000 geological map sheets of central NSW. (B) generalised localities for Devonian plant sites of eastern Australia mentioned in the text (BT, subsurface Bancannia Trough; DB, Darling Basin; LFB, Lachlan fold belt). (C) local geology for the fossil plants from the Gooloogong road cutting described in this paper (Grenfell 1:100,000 geological map sheet 8530; Dhp, Peaks Fm; Dhw, Bumberry Fm). Numbered localities mentioned in the text are: 1, Gooloogong road cutting; 2, Canowindra fossil fish site; 3, Iguana Creek/Genoa River; 4, Bindogundra, Parkes Syncline; 5, 'Dungeons' road cutting, Bumberry Syncline; 6, Burdekin Basin, Queensland; 7, Barraba, northern NSW; 8, Bunga Pinch quarry near Tathra, NSW south coast.

Fig. 2. External morphology of Gooloogong specimens. (A) *Leptophloeum rhombicum* cast, AMF.165612. (B) General view of rock slab AMF.57163, showing, on the right, specimen 1 lying on the surface and, on the left, specimen 3 (*Denglongia* cf. *hubeiensis*) dipping into the matrix. (C) AMF.57163, detail of preceding view showing a whorl of three branches surrounding the anatomically preserved central part of *Denglongia* cf. *hubeiensis*. (D) General view of rock slab AMF.57162 corresponding to Fig. 3A. (E) General view of rock slab AMF.57164 showing specimen 2. (F) Detail of the lower surface of rock slab AMF.57163 showing the outline of the anatomically preserved vascular cylinder of *Denglongia* cf. *hubeiensis*. (G) Detail of specimen 2 on rock slab AMF.57164 showing the stem node with two opposite branches and several emergences on the lower part. (H) AMF.57164, detail of specimen 2 showing the stem with parallel ridges. (I) *Archaeopteris macilenta*, leaf; AMF.165613. Scale bars : 2mm for (C, G, H, I); 5mm for (B, E); 10 mm for (A, F); 20 mm for (D).

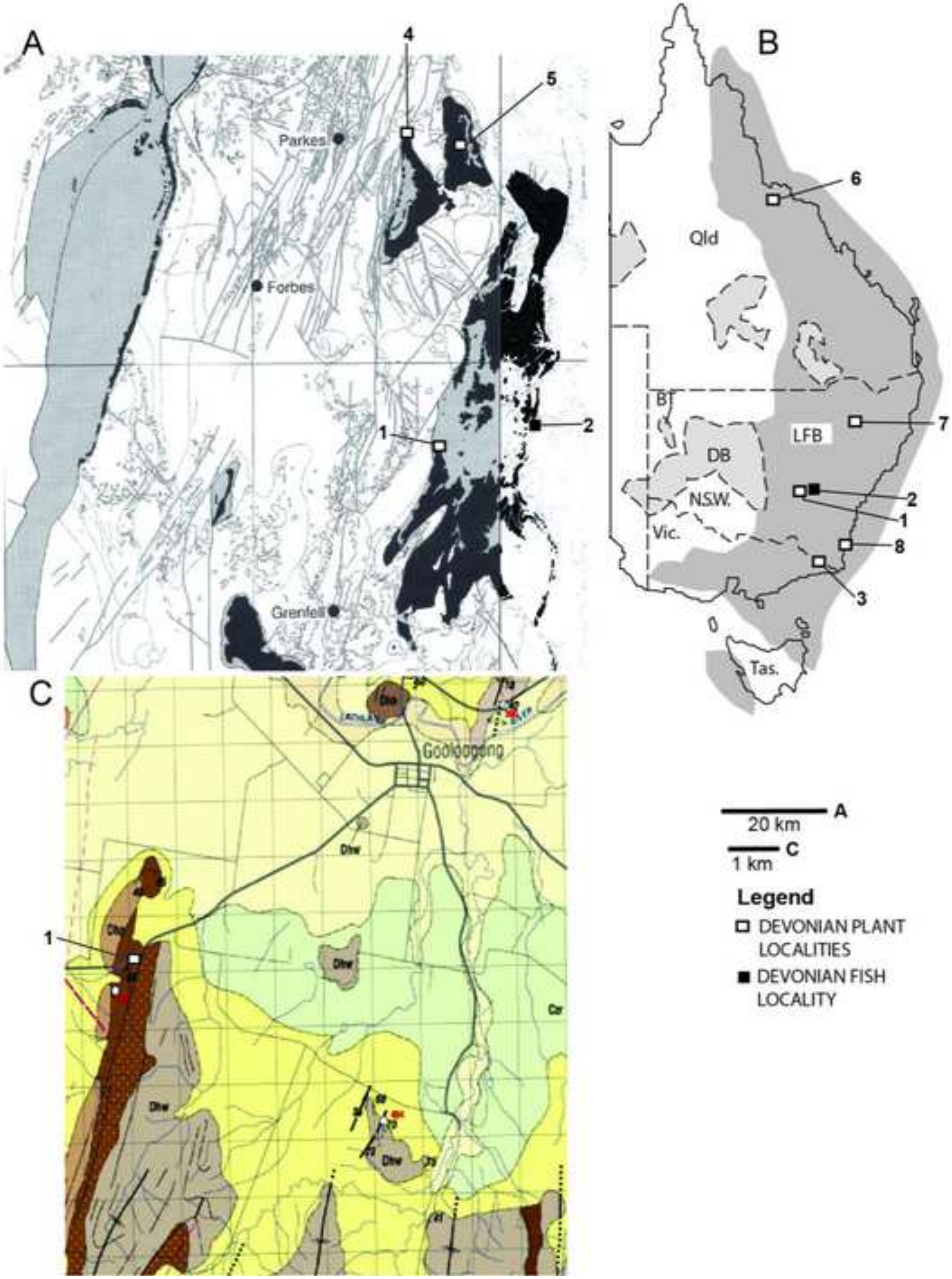
Fig. 3. Drawing of specimens on rock slabs AMF.57162 (in part), AMF.57163 and AMF57164. (A) AMF.57162. Specimen 1 with a single branch base attached. Specimen 2 with two opposite branches; the right branch is naked and produces a distal pair of opposite branches in the same plane. (B) AMF.57164. Counterpart of specimen 2. (C) AMF.57163. Counterpart of specimen 1 and upper surface of specimen 3. (D) Superposition of previous drawings showing the relative positions of the three axes.

Fig. 4. Anatomy of Gooloogong specimens. (A-C) *Denglongia* cf. *hubeiensis,* thin sections AM6968. (A) transverse section showing two ribs of the primary vascular cylinder; IC: inner cortex. (B) Detail of preceding view showing the distribution of tracheids at rib tips. (C) Longitudinal section showing scalariform tracheids. (D) *Archaeopteris* sp., AMF.165614, transverse section of the vascular system of a penultimate branch. (E) *Archaeopteris* sp., AMF.165615, transverse section of the vascular system of a penultimate branch. (F) *Callixylon* sp., transverse section of the vascular system of a root. (G) Detail of (D) showing a lobe of primary xylem and surrounding wood. (H) Detail of (F) showing the wood. (I) Detail of (F) showing the root stele. (J-L) Axis *incertae sedis*, AMF.6973, vascular cylinder in transversection. (J) General view of specimen. (K) Detail of preceding view showing the compressed wood and its smooth inner border. (L) Detail of preceding view showing the wood apparently devoid of rays. Scale bars : 500 µm for (F); 200 µm for (A, D, E, J); 100 µm for (B, C, G, H, I, K); 50 µm for (L).

Fig. 5. Compared vascular systems in transverse section of *Denglongia* cf. *hubeiensis* from Gooloogong and several iridopterids (E, G), transtitional cladoxylopsids (B, C), and cladoxylalean cladoxylopsids (D, F). (A) *Denglongia* cf. *hubeiensis* from Gooloogong, AMF.57163. (B) *Denglongia hubeiensis*, redrawn from Xue et al. (2010, Fig. 2a). (C*) Denglongia hubeiensis*, redrawn from Xue et al. (2010, Fig. 2e). (D) *Metacladophyton tetraxylum*, redrawn from Wang and Geng (1997, Text-fig. 5.2). (E) *Iridopteris eriensis*, redrawn from Stein (1982, Fig. 2). (F) *Polyxylon australe*, redrawn from Chambers and Regan (1986, Fig. 25). (G) *Arachnoxylon kopfii*, redrawn from Stein (1981, Pl. 1, fig. 2). All sections at same scale.

Fig. 6. Compared dissected leaves of *Archaeopteris*. (A) Specimen AMF.165613 from Gooloogong. (B) *A. macilenta*, redrawn from Beck (1971, Fig. 40) and Phillips et al. (1972, Pl. 36, fig. 7). (C*) A. sphenophyllifolia* from Arnold (1936, Pl. I fig. 6). (D) *A. notosaria*, redrawn from Anderson et al. (1995, figs. 30, 33, 37). (E) *A. fissilis*, redrawn from Nathorst (1904, Taf. 7 fig. 3). All leaves at same scale.

Fig. 7. Compared vascular systems in transverse section of archaeopterid branches (A-B, D-E) and roots (C, F). (A) Gooloogong penultimate branch, specimen AMF.165614. (B) Gooloogong penultimate branch, specimen AMF.165615. (C) Gooloogong root, specimen AMF.165616. (D) *Archaeopteris macilenta* penultimate branch, redrawn from Beck (1971, fig. 21). (E) *Archaeopteris macilenta* fertile ultimate branch, redrawn from Carluccio et al. (1966, fig. 1). (F) . Root of *Callixylon petryi*, redrawn from Beck (1953, fig. 13).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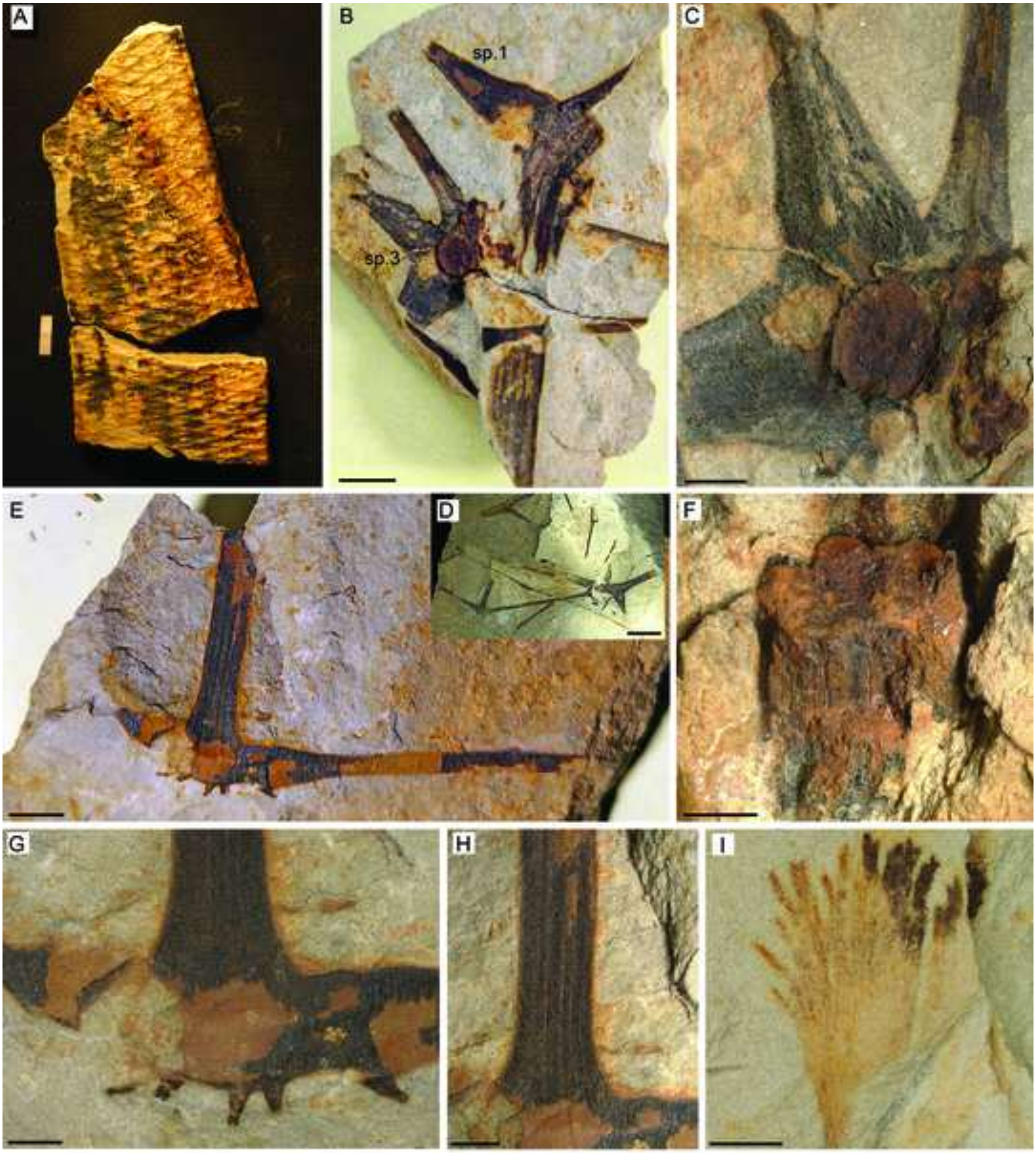

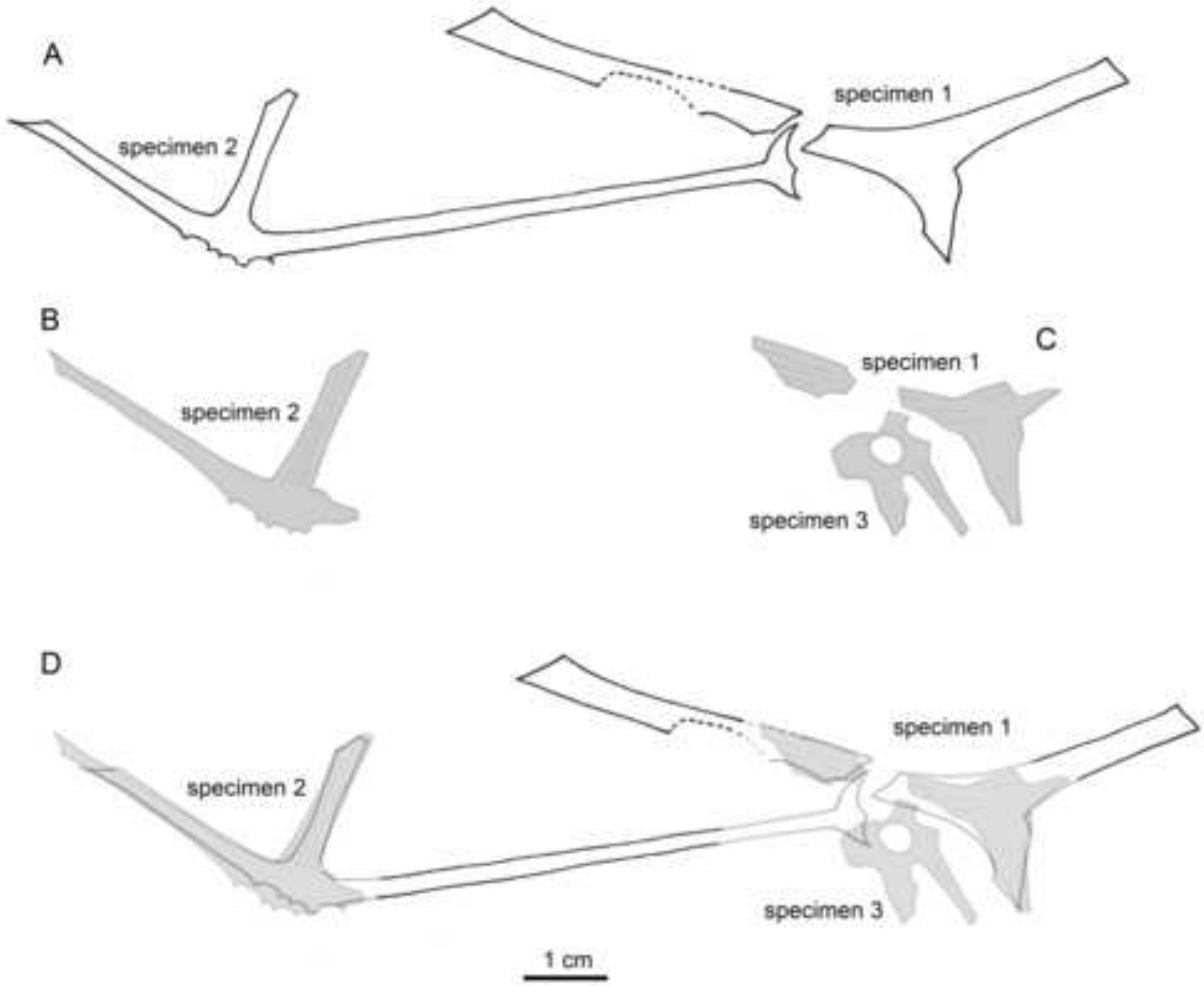
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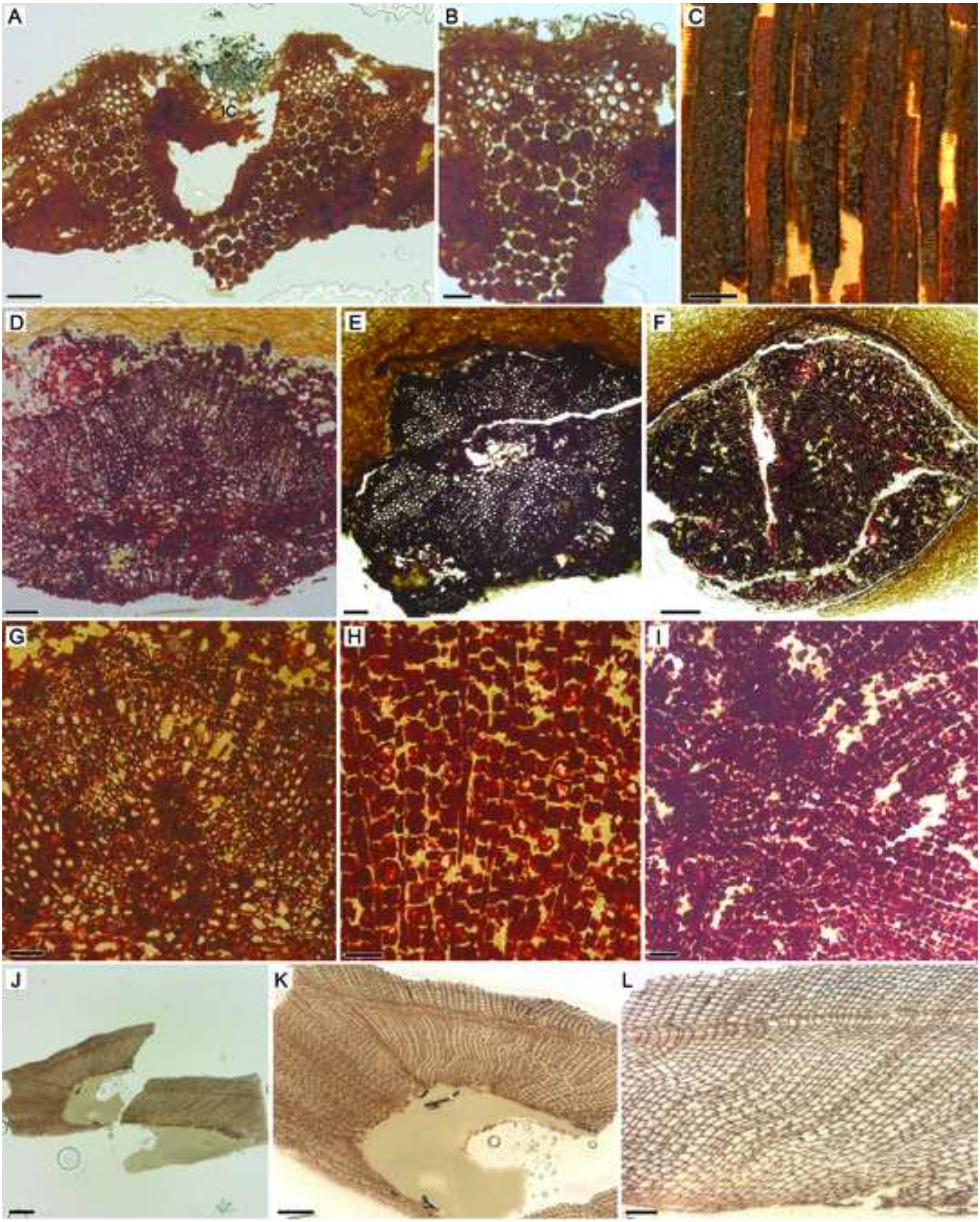
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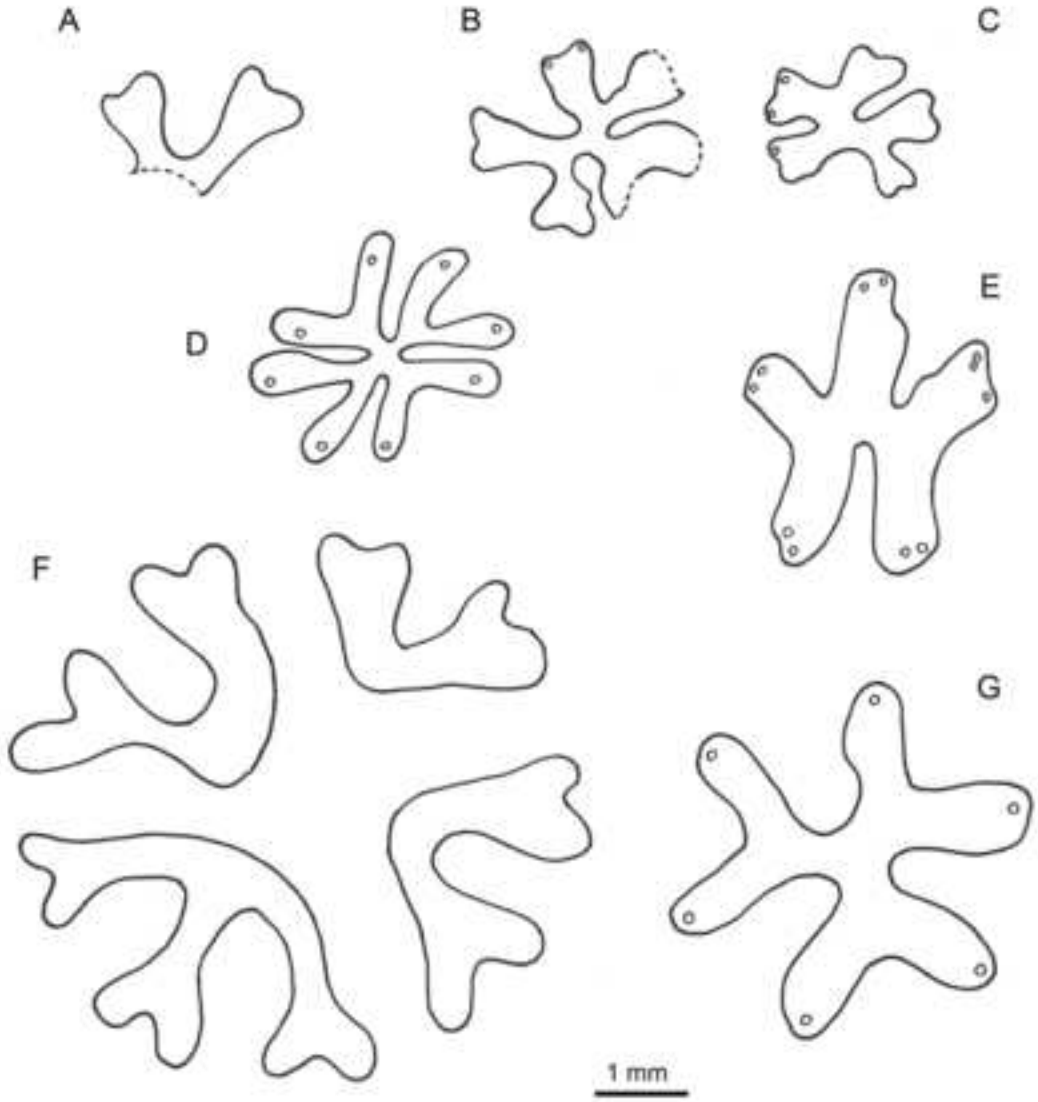
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Figure

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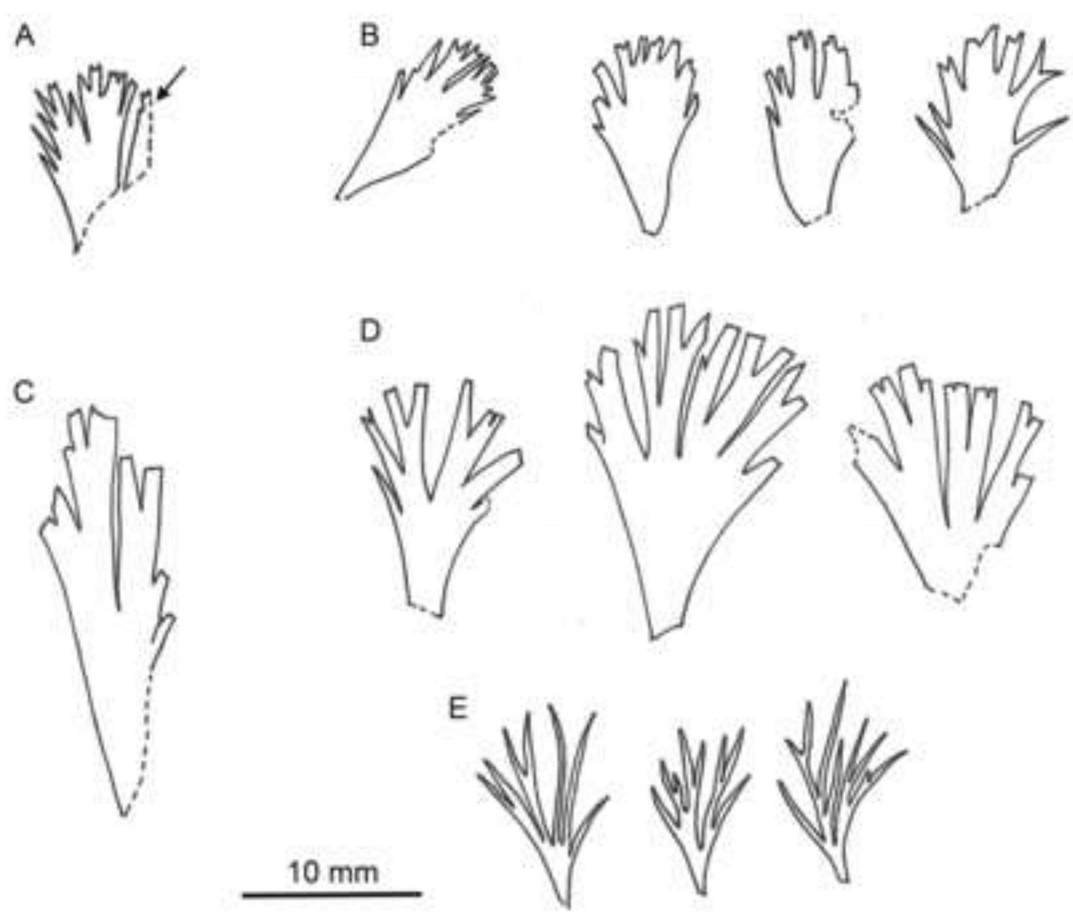

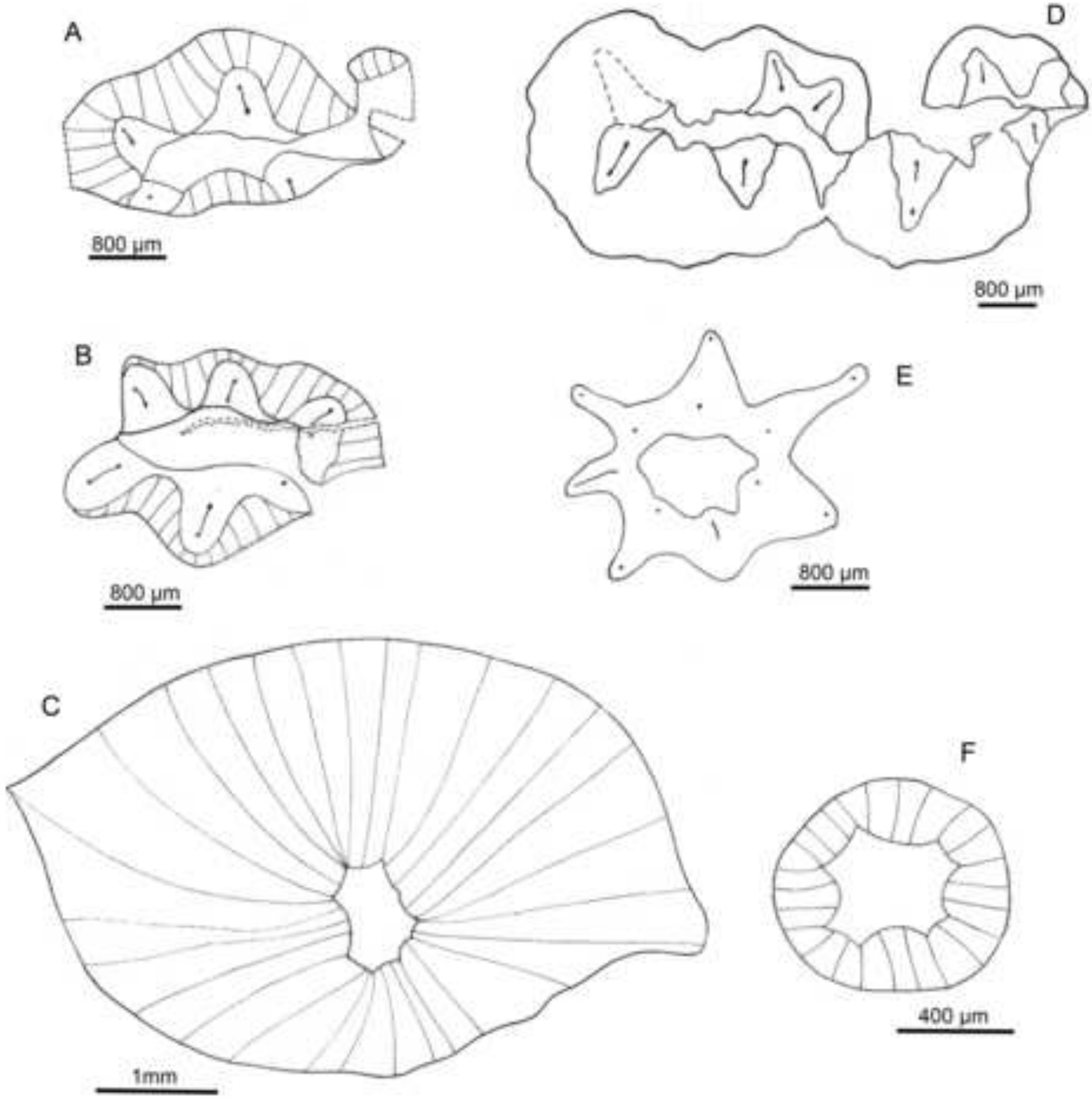
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Declaration of interests

☐The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☒The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Brigitte Meyer-Berthaud & Gaving C. Young reports financial support was provided by French Embassy in Australia. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.