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A Late Devonian plant assemblage from New South Wales, Australia: diversity and specificity

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ABSTRACT

Gondwanan floras of Late Devonian age are poorly known. In Australia, the rare studies that have been published on Late Devonian plants are old and need reinvestigation. This paper is an account of the plant macro- and micro-remains found in the Mandowa Mudstone at Barraba, New South Wales. According to the miospores, plants are late to latest Famennian in age. The record of anatomically preserved specimens is diversified, with nine taxa assigned to the Lycopsidea, Cladoxylopsida, Iridopteridales and Archaeopteridales. One specimen is referable to the spermatophytes. Several taxa are specific to Barraba, i.e., the lycopsid genera *Cymastrobis* and *Lycaugea*, the iridopteridalean genus *Keraphyton*, the cladoxylopsid species *Polyxylon australe*, and possibly a plant represented by a large *Hierogramma* branch showing exarch protoxylem strands. The adpression record is dominated by axes of the cosmopolitan lycopsid genus *Leptophloeum*. It also includes specimens interpreted as seed plants such as a possible ovule resembling *Pseudosporogonites*, and two types of foliage differing by their petiole width. One of this foliage consists of delicate fronds broadly comparable to those of *Cosmosperma*. The closest flora from Barraba is the late Famennian-earliest

Tournaisian flora of the New Albany Shale in eastern USA, suggesting floral connexion and comparable environmental conditions between Northern Gondwana and Southern Laurussia.

Keywords: Famennian, Gondwana, plant anatomy, Cladoxylopsida, Archaeopteridales, miospores.

1. Introduction

Gondwana, considered as the cradle of land plants (Gerrienne et al., 2016), is the largest landmass of the Palaeozoic. While the history of terrestrial plants in the Palaeozoic is mainly reconstructed from the Laurussian record (Taylor et al., 2009), recently supplemented by South Chinese data (Xiong et al., 2013), the size and palaeogeographic dynamics of Gondwana suggest a rich evolutionary history of its floras, which may have been decisive for the early evolution of vascular plants.

An interesting period in the Palaeozoic is the latest Devonian - earliest Carboniferous interval, when the basal members of such important groups as the Isoëtales, the 'true' ferns and the seed plants are found (Pigg, 2001; Phillips & Galtier, 2005; Prestianni & Gerrienne, 2010). It is also the time of the Hangenberg event, a biocrisis of first magnitude in the marine realm, associated with profound climatic changes and the onset of glaciations (McGhee et al., 2013; Kaiser et al., 2015; Boyer et al., 2021). The way in which the Hangenberg Event has manifested itself on the continents is more difficult to assess (Anderson et al., 2015), and evidence for a severe crisis in the terrestrial plant kingdom remains controversial (Streel & Marshall, 2006; Decombeix et al., 2011a; Cascales-Miñana, 2014; Prestianni et al., 2016; Denayer et al., 2019).

To address these issues, recent efforts have been made to document more systematically Gondwanan floras of Late Devonian - Early Carboniferous age from low and high palaeolatitudes. These studies have focused on localities in South America (Prestianni et al., 2015), Africa (Decombeix & Galtier, 2017; Gess & Prestianni, 2018; Prestianni & Gess, 2019; Tanrattana et al., 2019) and Australia (Galtier et al., 2007; Decombeix et al., 2011b; Evreinoff et al., 2017; Champreux et al., 2020; Meyer-Berthaud et al., 2021). The plant locality discovered at Barraba (New South Wales) in January 1964 by an amateur geologist, Mr. John Irving, is a rare Late Devonian locality in Australia yielding permineralized specimens associated with adpressions. Compared to the latter type of fossils, anatomically preserved plants are exceptional as they produce data on both the external morphology and internal structure (Locatelli, 2014). This is especially true for stems and branches, which are the

most frequent organs found at Barraba. Such fossils provide unique taxonomic information and are important tools for studying diversity patterns (Scott & Galtier, 1996).

This paper is an account of the late Famennian plants found at Barraba by Mr. Irving, and by ourselves, during three collecting trips. It summarizes the descriptions published so far, describes new anatomically preserved specimens, and gives a brief account of the affinities of the major types of plant remains preserved as adpressions. The generic composition of the Barraba flora is compared to that of other floras around the Devonian-Carboniferous boundary.

2. Material and methods

Barraba is a town in the New England region, north of Tamworth in New South Wales (Fig. 1A). Plants occur in the marine sediments of the Mandowa Mudstone Formation, in the Devonian part of the Tamworth Belt (Fig. 1B, C). This formation consists of a thick sequence of dark laminated mudstones interbedded with thin layers of whitish siltstones and sandstones (Vickery et al., 2010). The Mandowa Mudstone sites around Barraba have been assigned a Late Famennian age on different lines of evidence detailed in Wright (1988), Vickery et al. (2010), Evreinoff et al. (2017), Champreux et al. (2020). Recent sedimentological work on the Mandowa Mudstone, involving the study of this formation on the Manilla 1:100 000 geological map south of Barraba, suggested that the depositional environment was a distal marine shelf to continental slope (Vickery et al., 2010).

The locality that yielded permineralized plants occurs at the south-eastern edge of Barraba, at the confluence of Connors Creek and the Manilla River (locality 1 in Fig. 1D). The three other localities that we investigated occur upstream, along the banks of the Manilla River (localities 2-4 in Fig. 1D). They yielded only impression fossils. The fossil content of beds with limestone nodules expected to contain marine faunas, especially conodonts, was investigated. We did not find any conodont nor any other stratigraphic marker in these nodules. The only beds containing palynomorphs associated with adpressions were recovered at locality 4.

A list of the anatomically preserved specimens reported in this paper, of their repositories and identities, is provided in Table 1. Apart from *Polyxylon*, each taxon is represented by a single specimen. Field numbers BA- are used in this paper for the specimens we collected. All the other ones were collected by Mr. Irving. Museum registration numbers are available upon request to the Museum's Palaeontology Collection of the Australian Museum, Sydney. The main component of these fossils is calcium phosphate and some may contain pyrite in places (Champreux et al., 2020). Slides containing the miospores are housed in the Palynological collection, EDDy Lab., University of Liège, Belgium.

Thin-sections in the anatomically preserved specimens were observed with an Olympus SZX12 stereomicroscope, and two microscopes, an Olympus BX51 and a Keyence VHX. We used the Archimed and Keyence imaging software packages for acquiring digital photographs and measuring cells.

A brief description is given for the taxa that have already been published. Taxa which are new to the locality are described in more details and their affinities discussed.

3. Anatomically preserved specimens

3.1. Isoëtales, Lycopsidea

The anatomically preserved lycopsids are represented by two specimens, a cone and an axis, first mentioned in Chambers & Regan, 1986. They have been recently assigned to two new genera, *Cymastrobis* (type species *C. irvingii*; Evreinoff et al., 2017), and *Lycaugea* (type-species *L. edieae*; Meyer-Berthaud et al., 2021), both assumed to represent basal members of the Isoëtales.

3.1.1. *Cymastrobis irvingii*

Cymastrobis is represented by a large bisporangiate cone measuring 5 cm wide and exceeding 8 cm in length (Plate I, 1). The cone axis shows a medullated primary xylem cylinder showing an irregularly undulated outline. The sporophyll traces depart in a helical order from the grooves (Plate I, 2). Megasporophylls occur basally. The sporophyll-sporangium units show a long and narrow pedicel with an abaxial keel. The pedicel enlarges distally and forms a distal heel. Distal laminae are delicate and poorly preserved. Spores consists of a central body surrounded by an outer envelope which is not preserved. The megasporangia contain a large number of megaspores whose central body casts show imprints of more than a hundred of papillae arranged in rows around the trilete mark. The central body casts of the microspores show the marks of three interrational papillae.

3.1.2. *Lycaugea edieae*

The 8 mm wide fragment of axis representing *Lycaugea* is interpreted as producing deciduous leaves (Plate I, 3). Its outer surface shows helically arranged, widely separated, leaf bases. The specimen does not show any secondary tissue. It is characterized by a medullated primary xylem cylinder showing a smooth outline, and a wide middle cortex (Plate I, 3, 4). Leaf bases show a single abaxial parichnos.

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occasionally connect at their inner extremity (Plate I, 5, 6). Protoxylem strands are exarch in internodes, mesarch and associated with a cavity at nodes. Several cauline bundles participate to the emission of a branch vascular supply. Branch vascular supplies are bilaterally symmetrical and show at least six traces proximally.

3.3.2. *Cladoxylon* cf. *taeniatum*

Description - Specimen BA8 is a compressed, decorticated, and partially preserved portion of stem measuring 8 x 17 mm wide. About half of the stem may be missing (Pl. II, 1).

In transverse section, the vascular system of the stem consists of eleven radially elongated vascular bundles and four to six smaller internal bundles embedded in a ground tissue. All vascular bundles contain tracheids arranged in radial rows that are interpreted as secondary xylem (Pl. II, 2-4). The radially elongated bundles measure 0.3 to 0.7 mm wide and up to 2.8 mm radially. Some are fragmented into two radially aligned bundles of comparable length. They may also divide on their inner side to produce a small internal bundle. The radially elongated bundles show one mesarch protoxylem strand at each extremity (Pl. II, 3). The protoxylem strand located at the external tip is generally associated with a few large, thin-walled cells (Pl. II, 4). Additional protoxylem strands occur in the central part of the longest bundles (Pl. II, 2). The small internal vascular bundles show one or two centrarch protoxylem strands. Protoxylem tracheids are 18-30 μ m wide. There is no conspicuous zonation of the metaxylem tracheids, which are polygonal and up to 80 μ m wide (mean diameter = 53 μ m) in transverse section. The secondary xylem is relatively thick, up to 8 cells broad and appears slightly excentric in some bundles (Pl. II, 3). Secondary xylem tracheids tend to be rectangular and have dimensions comparable to those of the primary xylem tracheids. They range from 40 to 78 μ m in diameter (mean = 59 μ m). Each vascular bundle is separated from the ground tissue by a layer of cells that are generally less compressed than the neighbouring cells. They range from 55 to 75 μ m in width and may correspond to an endodermis (Pl. II, 3, 4). The ground tissue is an homogeneous parenchyma made of thin-walled cells that are often compressed and range from 45 to 100 μ m in diameter. This tissue does not show any special features like sclereid nests or sclerenchyma plates in its most external part.

The small vascular bundles external to the radially elongated bundles on each side of the specimen are interpreted as traces supplying at least two branches (Pl. II, 1). These branch vascular supplies are at about the same state of emission. The emission of a branch vascular supply involves four to five elongated vascular bundles. Each elongated bundle produces at least two successive branch traces in radial direction (Pl. II, 2). The number and spatial arrangement of the traces in a branch base is unknown. Individual branch traces are compressed and their original shape difficult to

characterize. They are elliptical, circular or triangular. They show one, two, or possibly three protoxylem strands. They are surrounded by secondary xylem.

Identification – Three non-pseudosporochnalean taxa show a vascular organisation close to that of specimen BA8, where the radially elongated bundles run parallel to each other, and where all bundles possess a secondary type of xylem. These are *Polypetalophyton wufengensis*, *Xenocladia medullosa*, and *Cladoxylon taeniatum*.

X. medullosina, the *Xenocladia* type-species, is represented by numerous specimens of Givetian age from New York state (USA) and Kazakhstan (Arnold, 1952; Lemoigne & Iurina, 1983). These specimens are larger in diameter and contain more numerous bundles than specimen BA8. They differ from the latter by several characters. First, the radially elongated bundles in *X. medullosina* may not be strictly linear and may show Y, U, or V shapes. Second, the protoxylem form solid strands and is not associated with thin-walled cells. Third, sclerenchyma plates are present between the radially elongated bundles. Finally, the traces produced by the elongated bundles are very small, devoid of secondary xylem, and they divide rapidly into two tangential traces.

P. wufengensis, the *Polypetalophyton* type-species, is based on Frasnian specimens from Hubei, South China (Hilton et al., 2003). First-order axes which are up to 10 mm wide are smaller than specimen BA8. They show a similar number of radially elongated bundles of comparable length but differ in the much larger amount of secondary xylem (i.e., rows of 15 cells in *Polypetalophyton*, 6 to 7 cells in specimen BA8). The anatomical pattern of branch trace emission is unknown in *P. wufengensis*. However, based on compression specimens, branches are borne helically in *P. wufengensis* whereas two branches, at least, are produced per node in the Barraba specimen.

The closest taxon to specimen BA8 is *Cladoxylon taeniatum* from the Tournaisian locality of Saalfeld, Germany (Unger, 1856; Solms-Laubach, 1896; Bertrand, 1935). A second species from Saalfeld, designated as *Cladoxylon dubium* by Solms-Laubach (1896), has been transferred to *C. taeniatum* and named *C. taeniatum* var. *dubium* by Bertrand (1935). Axes referred to as *C. cf. taeniatum* have also been described from a Tournaisian locality of Montagne Noire, France (Galtier, 1970; Scott et al., 1984). The specimens representing *C. taeniatum* var. *dubium* and *C. cf. taeniatum* are smaller than the *C. taeniatum* type-specimen and than specimen BA8.

In specimen BA8, as in *C. taeniatum*, *C. taeniatum* var. *dubium* and *C. cf. taeniatum*, the radially elongated bundles are linear and rarely connected to each other. The protoxylem strands at their external tip is associated with thin-walled cells and form the so-called "peripheral loops". The secondary xylem occurs all around the primary xylem and is thicker internally. Based on these characters, specimen BA8 can be assigned to *C. taeniatum*. The pattern of emission of the branch vascular supplies is unknown for the type specimen. In *C. taeniatum* var. *dubium* and *C. cf.*

taeniatum, this pattern involves up to four elongated bundles per branch like specimen BA8, but these bundles produce only one trace each, which are arranged in a single tangential row. Organotaxis in *C. taeniatum* var. *dubium* and *C. cf. taeniatum* is helical. In specimen BA8, which is larger, the traces leading to a branch are more numerous and they are arranged in at least two tangential rows; several branches are produced per node.

3.3.3. *Cladoxylon radiatum*

Description - Specimen BA4 is compressed, incomplete, and badly preserved. The specimen is entirely decorticated and measures about 4.5 x 10.5 mm in transverse section (Pl. II, 5). Contrary to specimen BA8, it does not show any secondary-type of tissue.

In transverse section, the stele consists of thirteen radially elongated vascular bundles, and 1-4 small internal bundles embedded in a ground tissue (Pl. II, 7). U- or V-shaped bundles are formed when neighbouring elongated bundles interconnect at their inner extremity (Pl. II, 5). Some elongated bundles divide at their inner end and produce internal bundles. No radially elongated bundle crosses the stele from side to side. The radially elongated bundles measure 0.2 to 0.35 mm wide and up to 3 mm radially. They show two mesarch protoxylem strand sometimes associated with thin-walled cells, one at each end (Pl. II, 6). Additional protoxylem strands are found in the longest bundles. The small internal vascular bundles show at least one centrarch protoxylem strand. There is no conspicuous zonation of the metaxylem tracheids, which are up to 45 μm wide in transverse section. The phloem is represented by a zone of badly preserved cells, which surrounds the metaxylem, and is especially conspicuous in the inner bundles. On the other hand, each vascular bundle is bounded externally by a prominent layer of rectangular thick-walled cells (Pl. II, 6). Thickenings are often greater on the tangential walls. From the position of this layer and the distinctive shape of its cells, and despite the fact that the radial walls are not necessarily thicker, we interpret it as an endoderm. The cells of the ground tissue range from 45 to 65 μm wide. This tissue is homogeneous and does not show any special cells nor features like sclereid nests in the outermost zones.

The four to six small vascular bundles external to the radially elongated bundles and occurring on one side of the axis are interpreted as branch traces (Pl. II, 7, 8). Their emission involves at least four neighbouring elongated vascular bundles. Evidence illustrated in Pl. II, 8 shows that the elongated bundles produce two successive branch traces in radial direction. Individual branch traces are either circular or elliptical and show one or two, or possibly three protoxylem strands.

Identification – Within the non-pseudosprochnalean taxa, it is with *Cladoxylon mirabile* and *Cladoxylon radiatum* that specimen BA4 shares the largest number of characters. These are the

radially elongated bundles that can be connected at their inner extremity, the lack of a secondary-type of tissue around the primary xylem, the external protoxylem strands associated with thin-walled cells forming the so-called "peripheral loops", and the possession of prominent endodermis cells (called "gaine périfasciculaire" by Bertrand, 1935). According to Bertrand (1935), *C. mirabile* differs from *C. radiatum* by its largest "peripheral loops" and the possession of scleric plates between the elongated vascular bundles. Specimen BA4 does not show any scleric plates.

3.3.4. *Hierogramma* sp.

Description – Specimen BA2 is flattened and measures 9 x 37 mm wide (Pl. III, 1). Despite its relatively large size, it does not show any secondary-type of tissue. Its cortex is almost entirely preserved.

In transverse section, the vascular system consists of more than fifteen tangentially elongated strands of different sizes embedded in a ground tissue. The strands are aligned in three parallel rows but it is uncertain to what extent this arrangement results from the deformation of the specimen. The strands on one face are lobate on their external surface (Pl. III, 2). The protoxylem is exarch and solid (Pl. III, 3). The metaxylem tracheids are large, ranging from 30 to 120 µm in diameter. The primary xylem is surrounded by a tissue, presumably the phloem, which consists of about 10 rows of small cells enclosing a layer of much larger elements (Pl. III, 3). The small cells are polygonal and measure 15-40 µm in diameter. The large elements are 60-80 µm wide radially and 25-45 µm wide tangentially. They may represent sieve cells.

The ground tissue, which is made of thin-walled cells, is highly compressed in the center, a little less in a 1.5-2 mm thick zone external to the vascular strands. Cells in this tissue are up to 130 µm wide. Isolated thin-walled cells of larger dimensions (up to 200 µm wide) and without any deformation are scattered throughout the ground tissue (Pl. III, 2). The surrounding cortex is 1.25 mm thick. Its small thick-walled cells have retained their polygonal shape. The largest ones are up to 90 µm in the vicinity of the ground tissue. They decrease to a width of 45 µm in the outermost cortical layers.

Identification – The xylem organized in tangentially elongated strands of specimen BA2 is a feature found in the branches of *Cladoxylon* known as *Hierogramma* or *Arctopodium*, the latter genus thought to be a synonym of *Hierogramma* (Solms-Laubach, 1896; Bertrand, 1935). The Barraba specimen is larger than the specimens reported in *Hierogramma* and *Arctopodium*, and it shows a larger number of vascular strands. Its large cells interspersed in the ground tissue are a trait also recorded in *C. taeniatum*, *C. mirabile* and *Hierogramma* (Bertrand, 1935). In addition, its phloem comprised of small cells enclosing a row of large cells presumed to be sieve cells is similar to that

described in *Hierogramma* (Bertrand, 1935). The main difference between specimen BA2 and *Hierogramma*, or *Arctopodium*, lies in the protoxylem strands that are exarch in the former whereas they are mesarch and associated with parenchyma ("peripheral loops") in the latter genera. With regard to its relatively large size, specimen BA2 may have been a branch produced by a larger cladoxylipsoid stem than the specimens of *C. cf. taeniatum* and *C. radiatum* from Barraba described above. We assign it here to *Hierogramma* sp. In Australia, small specimens of *Hierogramma* sp. that are no more than 10 mm wide have been reported, but not illustrated, from the mid-Tournaisian locality of Ruxton in Queensland (Galtier et al., 2007).

3.4. Archaeopteridales, Progymnospermopsida

3.4.1. *Callixylon* sp.

Description – Specimen BA10 consists of wood fragments taken from a log measuring about 10 cm wide that remained on site. The log was highly compressed, partly coalified and brittle, a preservation unfavorable for thin-sections. The collected fragments were observed in scanning electron microscopy. Most views correspond to radial sections. Tracheids range from 35 to 60 µm in diameter (Pl. III, 7, 9). Bordered pits with slit-like openings are multiseriate and arranged in groups (Pl. III, 8). Rays are low, parenchymatous and devoid of any ray tracheid (Pl. III, 9). Tangential views are rare. The few observable rays in tangential section appear inconspicuous, uniseriate and short.

Identification – With its bordered pits arranged in groups on the radial walls of tracheids, specimen BA10 is assignable to *Callixylon*, the name given to the permineralized trunks, main branches and roots of the Archaeopteridales. *Callixylon* woods with narrow rays characterized by ray tracheids that are lacking or rare are affiliated to the informal "Trifilievii" group of Orlova & Jurina (2011), which includes *C. trifilievii* and several junior synonyms, *C. brownii* and *C. whiteanum*. Woods referable to this group are known from all the palaeocontinents where *Callixylon* has been reported (Tanrattana et al., 2019). Without any information on its stelar characters, the Barraba log cannot be referred to a particular species. We call it *Callixylon* sp.

3.5. Pteridospermales, Spermatophytes

3.5.1. *Kalymma grandis*

Description - Specimen BA1 is preserved over about half of its diameter (Pl. III, 4). It is 9 mm wide in its largest dimension. In transverse section, it shows an incomplete ring of 11 primary vascular bundles regularly distributed at the periphery of a ground tissue whose central part is not preserved. The specimen is bounded by a sparganum cortex, i.e. consisting of radial bands of thin-walled cells alternating with bands of narrow thick-walled cells, and by a subepidermal tissue consisting of a few rows of narrow cells (Pl. III, 5). The specimen does not show any secondary tissue.

The preserved part of the ground tissue is homogeneous. It is made of relatively wide thin-walled cells that range from 35 to 160 μm in diameter, the majority measuring 80 to 100 μm wide. Some scattered cells in this tissue show a black content.

Most vascular bundles are missing and replaced by a lacuna (Pl. III, 5). In transverse section, individual lacunae are radially elongated, about twice longer than wide. They measure up to 900 μm radially and 400 to 550 μm tangentially. The vascular bundles are separate except for two that are connected on their inner side (Pl. III, 4). An empty V-shaped lacuna suggest the occurrence of a second pair (Pl. III, 5). Tracheids in the preserved bundles are 20-70 μm in diameter, the smaller ones in peripheral position. Each bundle shows two mesarch protoxylem strands. One occurs at the external tip, the other in lateral position (Pl. III, 6).

The sparganum cortex is 550 to 780 μm thick (Pl. III, 5). It is thicker on the convex part (Pl. III, 4). The individual sclerenchyma bands are 170 μm wide. They range from 270 to 470 μm radially in the thinnest part of the cortex, and are up to 600 μm in the thickest part where they eventually split in two. Sclerenchyma cells are 16 to 40 μm wide, most around 25-30 μm . The parenchyma cells between the sclerenchyma plates are larger, from 25 to 75 μm in diameter, a large number around 50 μm . The subepidermal cells external to the sparganum decrease in diameter, from 45 μm near the sclerenchyma plates to 25 μm outside.

Identification - Specimen BA1 is assignable to *Kalymma* (Unger) Braun & Wilde (Unger, 1856; Braun & Wilde, 2001), a genus corresponding to anatomically preserved petioles and rachises of calamopityacean affinities (Sebby & Matten, 1969). Such petioles and rachises are characterized by a subepidermal tissue of sparganum-type. The vascular bundles, which tend to be separate in the proximal parts of *Kalymma* petioles and connected in more distal portions of the fronds, are arranged in a ring or a C-shaped configuration within a parenchymatous tissue. *Kalymma* petioles may form a wide angle with their parent axis and are often broken at their insertion level (Long, 1964; Galtier, 1974). The Barraba specimen, which is preserved on one side only and has a majority of separate vascular bundles, may correspond to the proximal part of a petiole, close to the level of attachment to the stem from which it was torn. In this case, the thickened part of the sparganum would be on the abaxial side, a feature probably involved in the support of the frond.

Up to ten species of *Kalymma* have been described since Unger's (1856) first report of the genus. They range from the latest Devonian to the early Mississippian and have been reported from localities in Europe (Germany, southern France, Scotland) and eastern USA (Kentucky, Indiana, Tennessee).

Studies led by Sebby & Matten (1969), Galtier (1974) and Matten & Trimble (1978) showed that the shape, size, number, and spacing of the vascular bundles vary along the fronds and must be used with caution for taxonomic purposes. Matten & Trimble (1978) reduced the number of *Kalymma* species to three, *K. grandis*, *K. resinosa* and *K. tuediana*. The type-species *K. grandis* (Braun & Wild, 2001), was synonymized with *K. striata*, *K. debilis*, *K. hippocrepis*, *K. lirata* and *K. auricula*. *Kalymma resinosa* was synonymized with *K. minuta*. Specimen BA1 shows the largest number of characters in common with *K. grandis*. Indeed, the ground tissue in *K. grandis* is uniform and may include cells with a dark content. Xylem bundles have a mesarch maturation and show 2-5 protoxylem strands that may occur laterally, on one side of the bundles. In contrast, the ground tissue of *K. resinosa* is characterized by lysigenous cavities, and *K. tuediana* is distinguished by its exarch maturation of the xylem. Specimen BA1 can hardly be compared with *K. coumiacensis*, a species represented by a single specimen corresponding to a more distal part of frond bearing pinnules and showing fused vascular bundles (Galtier, 1981). Finally, the specimen referred to as *Kalymma* sp. from Germany reported by Braun & Wilde (2001) differs from the Barraba specimen by the possession of numerous sclerotic nests in the ground tissue. The Barraba specimen is the first evidence of the genus in Australia, and the first evidence of the Calamopityaceae in a Late Devonian deposit of Gondwana.

4. Adpression specimens

The largest fossils, such as the ones figured in Plate IV, 1, 3, 6, 7, were too brittle to be removed and transported. They remained on site. The most abundant specimens found at the four Barraba localities are adpressions and casts of vegetative axes of *Leptophloeum* (Plate IV, 1, 2). All the other specimens do not show sufficient diagnostic characters to be accurately identified. Axes showing large ribbing and occasional nodes on the external surface are tentatively assigned to the Cladoxylopsida when large (Plate IV, 3), to the Sphenopsida when small (Plate IV, 4). The branching structure with an enlarged base and without any ribbing on the surface illustrated in Plate IV, 5 is suggestive of a pteridosperm petiole base. If permineralized, such a structure could be referable to *Kalymma*. The 3-mm wide axis figured in Plate IV, 6 divides dichotomously and then alternately in the resulting branches (Plate IV, 7). The interval between alternate nodes is 3 cm (Plate IV, 7). This

delicate specimen is morphologically comparable to the bifurcate fronds of Famennian seed plants reported from Chinese localities like *Yiduxylon trilobum* from Hubei (Wang & Liu, 2015), and *Cosmosperma polyloba* from Zheijiang (Liu et al., 2017). The narrowness of the rachises and the length of the 'internodes' between the distal order of rachises in the Barraba specimen make it closer to *Cosmosperma*. The affinities of this probable seed plant remain uncertain, however, in view of the lack of information on its anatomy and distal appendages, whether fertile or sterile. Finally, a single specimen figured in Plate IV, 8 may represent a seed terminating a relatively long and narrow axis. The genus *Cosmosperma* mentioned above has uniovulate cupules which, unlike the Barraba specimen, show distinct cupulate lobes distally, and may be borne in pairs on shorter stalks (Wang et al., 2014; Liu et al., 2017). The cupulate seeds of *Calyscosperma* from the Famennian of Zheijiang are borne singly at the tip of long stalks (Liu et al., 2018). However, they are larger than the Barraba specimen and, like *Cosmosperma*, they show up to 16 separate cupule lobes distally. The Barraba specimen does not show the small cupule lobes of *Latisemenia*, another Famennian genus from Zheijiang (Wang et al., 2015). It rather resembles the *Pseudosporogonites* seeds with diminutive cupules recorded from different Famennian deposits of Europe and USA, especially the species *P. quadrapartitus* from South Wales (Hilton & Edwards, 1996; Prestianni et al., 2013).

5. Miospores

The miospores of locality 4 are not abundant but relatively well diversified (Plate V, 1-9). Their colour is brown to dark brown. Most have no stratigraphic significance, but two of them are very well-known and have a great value for the Famennian. These are *Retispora lepidophyta* (Kedo) Playford 1976 (Plate V, 5, 6) and *Verrucosisporites nitidus* Playford 1964 (Plate V, 8, 9). Both are the eponym species of the LN Biozone (i.a. Streel et al., 1987, 2000), which is the youngest of the Famennian. Its top characterises the D-C boundary. No miospore of a younger age has been found in the sediments collected at locality 4. The age of the sample and its megaflora is thus clearly late to latest Famennian.

6. Discussion

Of the five genera that are not specific to Barraba, *Callixylon* and *Polyxylon* are unknown above the early Tournaisian and *Cladoxylon*, *Hierogramma* and *Kalymma* are unknown before the

late Famennian. This is in agreement with the Late Famennian age of the Mandowa Mudstone beds at Barraba, and with the age of the palynoflora found at locality 4.

Anatomically preserved specimens are rare at Barraba, but they are surprisingly diverse. All the major groups of plants of the latest Devonian are present, with two genera of isoëtalean lycopsids (*Cymastrobis*, *Lycaugea*), three cladoxyloids (*Polyxylon*, *Cladoxylon*, *Hierogramma*), the archaeopteridalean progymnosperm *Callixylon*, and a seed plant represented by its *Kalymma* petiole. The Iridopteridales, whose stratigraphical extension beyond the Frasnian was considered uncertain, are represented by *Keraphyton*. Seven out of the eight genera recognized in this allochthonous assemblage correspond to spore-producing plants that may have lived in coastal habitats or along river banks.

Remains preserved as adpressions are abundant and appear diversified, despite the fact that most of them cannot be precisely identified. They complement the information provided by the permineralized specimens. Thus, together with *Leptophloeum*, the Lycopsida are represented by three different plants at Barraba. The seed plants seem to be better represented in the adpression record, with a possible acupulate ovule and two types of fronds differing in the size of their petioles (compare petiole width in Pl. IV, 5 and 6).

Few detailed studies have been carried out on the Late Devonian floras from Australia (Hill et al., 1999). Those dealing with anatomically preserved remains are especially rare, with one anatomically preserved stem from Taberrabbera (Victoria), tentatively assigned to the sphenopsids (Douglas, 1960). The best known adpression assemblages consists of those from Genoa River in the county of Auckland, New South Wales, and Iguana Creek, on the Mitchell River in Gippsland, Victoria, which may have been contemporaneous (McCoy, 1876; Dun, 1897). They share the occurrence of *Archaeopteris* together with remains improperly called "*Cordaites australis*", which resemble the basal parts of abscised petioles or branches of uncertain affinities. In both localities, fragments of compound leaves have been assigned to *Sphenopteris*, *S. carnei* at Genoa River, and *S. iguanensis* at Iguana Creek. These fossils are unlike the fronds of the fern genus *Ellesmeris*, the single zygoterid type of fern of Late Devonian age with laminated pinnules (Hill et al., 1997). It is thus more likely that *S. carnei* and *S. iguanensis* corresponded to seed plant foliage. The Genoa River assemblage also includes *Barinophyton*, a genus of uncertain affinities (Hao & Xue, 2013). Gould (1975) stated that the plant beds at Genoa River might have been Frasnian but the occurrence of *Sphenopteris* would be in favor of a Famennian age. Apart from *Archaeopteris*, the Genoa River and Iguana Creek plants differ from those of the Barraba assemblage, which, as far as we know, lacks Barinophytales and sphenopterid-type foliage.

Anatomically preserved floras spanning the late Famennian to the early-mid Tournaisian have been described mainly from the palaeocontinent Laurussia (e.g., the floras from Ireland, and

from the New Albany Shale in eastern USA) and the European terranes (e.g., the floras from Saalfeld in Germany, and Montagne Noire in southern France). It is with the New Albany Shale floras that the Barraba plant assemblage shares the greatest number of similar taxa. The mid-tournaisian floras from Saalfeld and Montagne Noire are the youngest and are preserved in marine sediments like the Barraba specimens. They have *Cladoxylon*, *Hierogramma* and *Kalymma* in common with the Barraba plant assemblage, but their lycopsids are different and they do not show any archaeopteridalean progymnosperms (Galtier, 1970; Meyer-Berthaud, 1984). In Ireland, three plant localities dated of the latest Famennian have been recorded, Kiltorcan, Ballyheigue and Hook Head (Jarvis, 1990). They represent floodplain and fluviatile environments (Matten, 1989). Apart from *Archaeopteris* the adpressions at Kiltorcan, which include lycopsid remains of *Cyclostigma/Jurinodendron* and the platyspermic seed *Spermolithus*, are unlike any taxa from Barraba (Holland, 1981; Chaloner et al., 1977). Ballyheigue yielded anatomically preserved specimens, all assignable to the seed plants (Matten et al., 1984). The only taxon resembling a plant from Barraba is the lycopsid *Wexfordia hookense*, from Hook Head, which has been compared with *Lycaugea edieae* (Matten, 1989; Meyer-Berthaud et al., 2021). The late Famennian to early Tournaisian floras from the New Albany Shale were recovered from marine sediments. They have four genera in common with the Barraba plant assemblage, *Polyxylon*, *Hierogramma*, *Callixylon* and *Kalymma* (Read & Campbell, 1939; Hoskins & Cross, 1952). *Cladoxylon* is not reported in the New Albany Shale but *Hierogramma* suggests its occurrence. In addition, resemblances were noted between the lycopsids from Barraba and two taxa from the New Albany Shale, *Lycaugea* and the Cichan & Beck (1987)'s specimen from Kentucky on one hand, *Cymastrobis* and *Flemingites noei*, also from Kentucky (Mathews, 1940) on the other hand (Evreinoff et al., 2017; Meyer-Berthaud et al., 2021). The Barraba plant assemblage differs from the Famennian floras of South China (Xiong et al., 2013) with which it shares only the cosmopolitan genera *Callixylon* and *Leptophloeum*, and, possibly, a spermatophyte with delicate fronds of the *Cosmosperma*-type. These statements are consistent with earlier considerations of a cosmopolitan character of the Late Devonian floras from Australia, tempered by the evidence of specific taxa suggesting some level of provinciality at the genus or species level (Hill et al. 1999; Playford in Talent et al., 2000). They are also consistent with a palaeogeographic connection between Gondwana and Southern Laurussia during the late Famennian whereas geographic barriers may have prevented extensive floral exchanges between the eastern part of Gondwana and South China at this time (Torsvik & Cocks, 2013).

7. Conclusion

- Plant macroremains recovered from the Mandowa Mudstone around Barraba consist of adpressions and permineralized specimens that provide additional information on the composition of the regional flora. The miospores indicate a late to latest Famennian age for these plants.
- The record of anatomically preserved specimens is dominated by spore-producing plants. Among them are two lycopsid genera, *Cymastrobis* and *Lycaugea*, and an iridopteridalean genus, *Keraphyton*, that are unknown elsewhere. The cladoxylopsid species *Polyxylon australe* and the one represented by a large *Hierogramma* are also specific to this flora. The single specimen assignable to the seed plants is a petiole base referable to *Kalymma*, a genus so far recorded in Southern Laurussia.
- The record of adpressions is also varied and includes more specimens of probable seed plant affinities. The latter consist of a possible acupulate ovule superficially resembling the genus *Pseudosporogonites* from Southern Laurussia, and two types of foliage, one being represented by delicate fronds broadly comparable to those of the genus *Cosmosperma* from South China.
- The Barraba plant assemblage is closer to the flora of the New Albany Shale than to any other Famennian-Early Carboniferous floras of Southern Laurussia. It differs from the contemporaneous floras of Southern China, with which it shares only the cosmopolitan genera *Leptophloeum* and *Callixylon*, and possibly a seed plant. This palaeogeographical considerations are consistent with floral connections and close environmental conditions between the northern border of Gondwana and Southern Laurussia, whereas geographic barriers may have prevented extensive floral exchanges with South China.

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TABLE LEGEND

Table 1. List of specimens described in this paper.

FIGURE LEGEND

Fig. 1. Maps of the Barraba plant locality. A. Map showing Barraba in New South Wales. B. Map of
Devonian outcrops of southeastern new England; modified from Pedder (1967). C. Map of Devonian
(Noumea beds and Mandowa Mudstone) and Lower Carboniferous outcrops of the Barraba area
(From Manilla 1:100 000 geology sheet 9036). D. Locations of the four investigated plant localities at
Barraba.

PLATE LEGENDS

Plate 1. Anatomically preserved specimens from locality 1, Barraba, NSW. All figures in transverse
section except 1.

1-2. *Cymastrobis irvingii*, holotype NMVP 161998. 1. Cone in external view; 2. Detail of the cone axis
showing the undulated border of the primary xylem and emission of a sporophyll trace.

3-4. *Lycaugea edieae*, holotype NMVP 161999.0. 3. General view of axis showing medullated stele,
three-zoned cortex and small leaf bases at periphery; 4. Detail showing the smooth border of the
primary xylem and sporophyll traces in the inner cortex.

5-6. *Polyxylon australe*, F65557. 5. General view of axis showing the ring of radially elongated
vascular bundles; 6. Detail of the dichotomizing extremity of a vascular bundle.

7-9. *Keraphyton mawsoniae*, holotype MMF44986. 7. General view of axis showing the actinostelic
vascular system, and cortex on the bottom side; 8. Detail of a dividing rib; 9. Detail of the central part
of the stele.

fr: fundamental rib; lb: leaf base; st: sporophyll trace; mc: middle cortex; x1:primary xylem.

Plate 2. Anatomically preserved specimens from locality 1, Barraba, NSW. All figures in transverse section.

1-4. *Cladoxylon* cf. *taeniatum*, specimen BA8. 1. General view of axis; 2. Detail of radially elongated bundles producing traces in two rows; 3. Detail of radially elongated bundles and ground tissue; 4. Detail of two radially elongated bundles showing the protoxylem strands associated with a lacuna in the primary xylem, and the surrounding secondary xylem.

5-8. *Cladoxylon radiatum*, specimen BA4. 5. General view of axis; 6. Detail of two radially elongated bundles surrounded by a conspicuous layer of endodermis cells, and showing the protoxylem strands associated with a lacuna in the primary xylem; 7. Detail of radially elongated bundles and a row of elongated traces; 8. Detail of traces in two rows ; bt1 and bt2 are successive branch traces produced by a radially elongated bundle.

bt: branch trace; en: endodermis; ib : internal bundle ; px: protoxylem; x2:secondary xylem.

Plate 3. Anatomically preserved specimens from locality 1, Barraba, NSW. Figures 1-6 in transverse section; figures 7-9. MEB photographs of wood in longitudinal section.

1-3. *Hierogramma* sp., specimen BA2. 1. General view; 2. Detail of a lobate vascular strand; 3. Detail of a vascular strand showing the primary xylem and surrounding phloem with a row of large cells between two layers of smaller elements.

4-6. *Kalymma grandis*, specimen BA1. 4. General view; 5. Detail showing two missing vascular bundles embedded in a ground tissue, and the sparganium cortex on the outside; 6. Two vascular bundles after separation, each one with two protoxylem strands.

7-9. *Callixylon* sp., specimen BA10, radial MEB views. 7. Radial walls of tracheids showing multiseriate bordered pits in groups; 8. Detail of a group of bordered pits showing slit-like openings; 9. detail of a ray showing four rows of parenchyma cells.

ph: phloem; px: protoxylem; x1:primary xylem.

Plate 4. Specimens preserved as adpressions.

1-2. *Leptophloeum* axes. 1. Dichotomous axis showing different levels of decortication, locality 1; 2. Specimen showing leaf bases that are as wide as high, locality 2.

3. Large axis of putative cladoxylopsid affinities, locality 1. Possible node at arrow.

4. Small axis of putative sphenopsid affinities, locality 2.

5. Enlarged petiole base of putative seed plant affinities, locality 2.

6-7. Frond of putative seed plant affinities, locality 1. 6. Proximal part showing a petiole branching dichotomously, producing two primary rachises; 7. Primary rachis at top of previous figure showing departure of three secondary rachises arranged alternately at arrows.

FIG.1

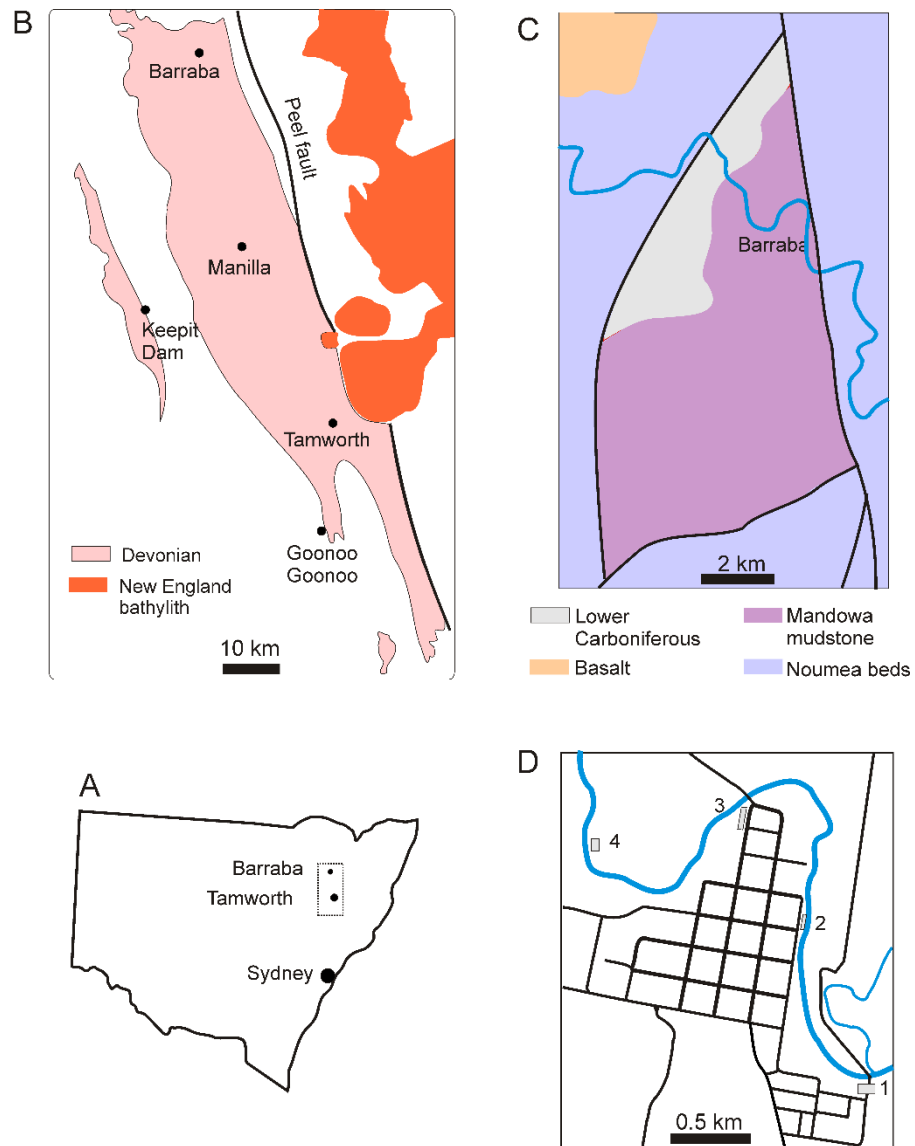


PLATE 1

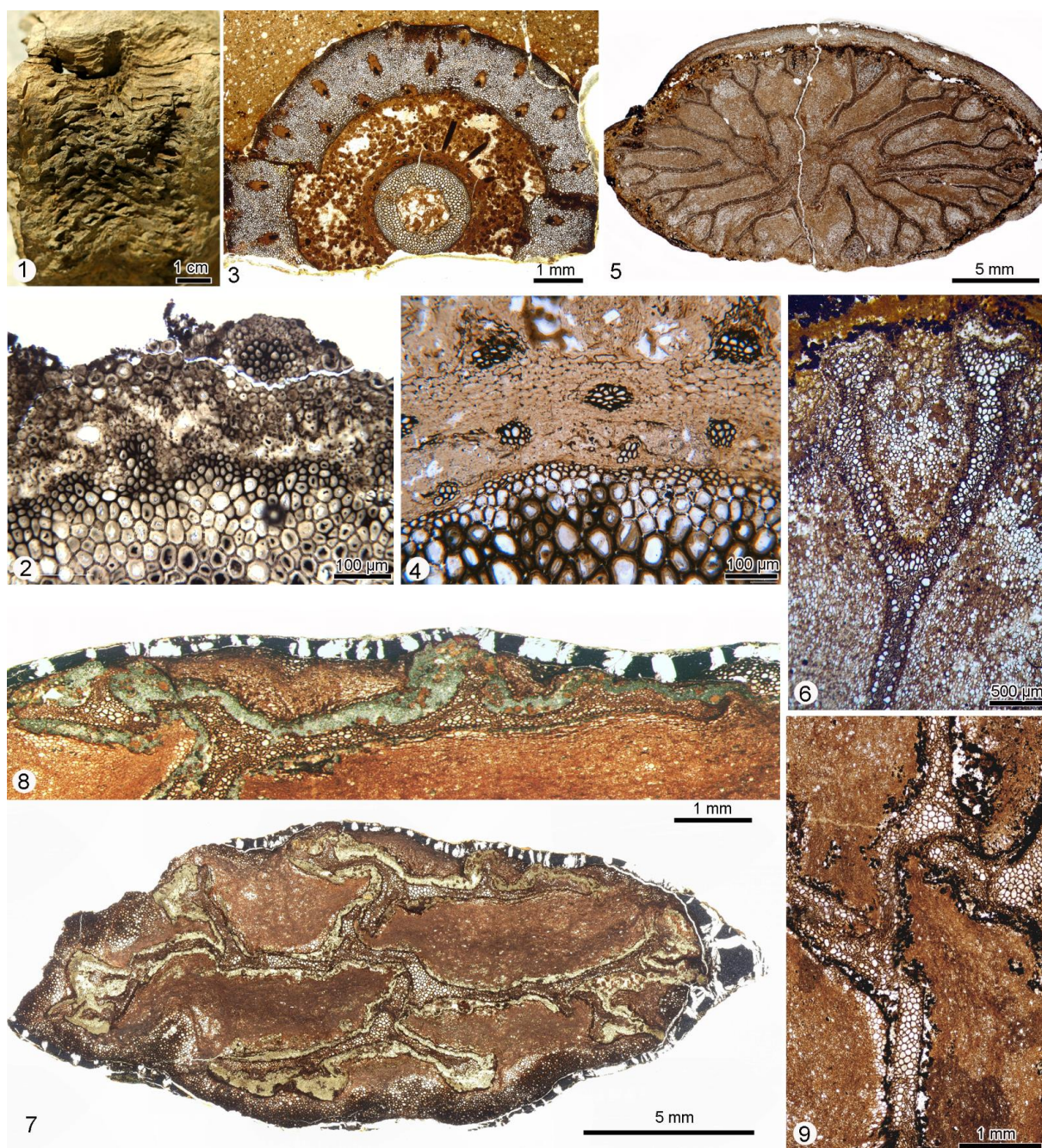


PLATE 2

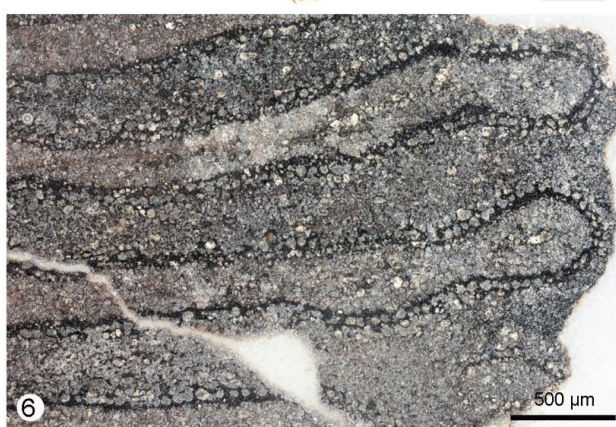
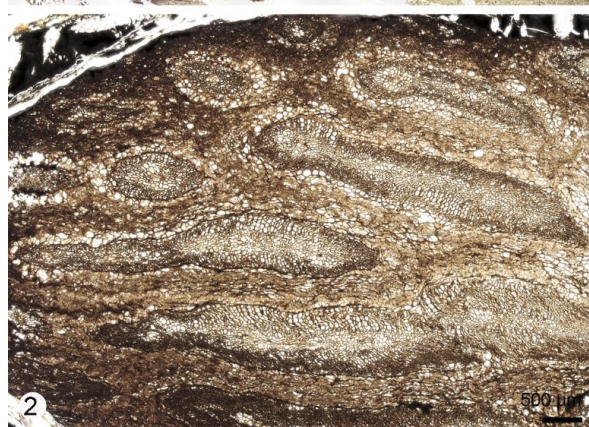


PLATE 4

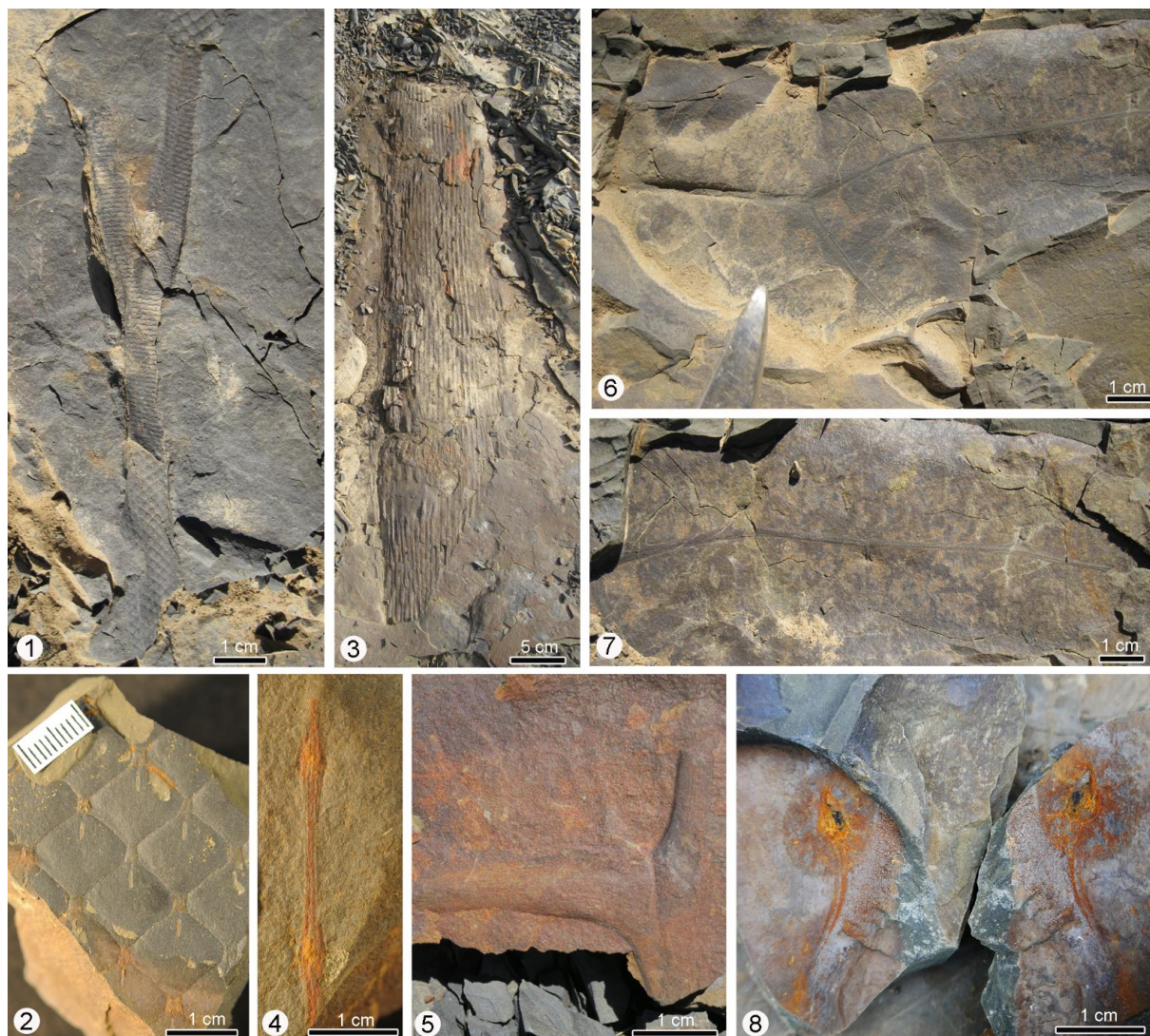


PLATE 5

