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

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20 **ABSTRACT**

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

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

36

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

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39

40 **1. Introduction**

41

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

48 An interesting period in the Palaeozoic is the latest Devonian - earliest Carboniferous
49 interval, when the basal members of such important groups as the Isoëtales, the 'true' ferns and the
50 seed plants are found (Pigg, 2001; Phillips & Galtier, 2005; Prestianni & Gerrienne, 2010). It is also
51 the time of the Hangenberg event, a biocrisis of first magnitude in the marine realm, associated with
52 profound climatic changes and the onset of glaciations (McGhee et al., 2013; Kaiser et al., 2015;
53 Boyer et al., 2021). The way in which the Hangenberg Event has manifested itself on the continents is
54 more difficult to assess (Anderson et al., 2015), and evidence for a severe crisis in the terrestrial plant
55 kingdom remains controversial (Streele & Marshall, 2006; Decombeix et al., 2011a; Cascales-Miñana,
56 2014; Prestianni et al., 2016; Denayer et al., 2019).

57 To address these issues, recent efforts have been made to document more systematically
58 Gondwanan floras of Late Devonian - Early Carboniferous age from low and high palaeolatitudes.
59 These studies have focused on localities in South America (Prestianni et al., 2015), Africa (Decombeix
60 & Galtier, 2017; Gess & Prestianni, 2018; Prestianni & Gess, 2019; Tanrattana et al., 2019) and
61 Australia (Galtier et al., 2007; Decombeix et al., 2011b; Evreinoff et al., 2017; Champreux et al., 2020;
62 Meyer-Berthaud et al., 2021). The plant locality discovered at Barraba (New South Wales) in January
63 1964 by an amateur geologist, Mr. John Irving, is a rare Late Devonian locality in Australia yielding
64 permineralized specimens associated with adpressions. Compared to the latter type of fossils,
65 anatomically preserved plants are exceptional as they produce data on both the external morphology
66 and internal structure (Locatelli, 2014). This is especially true for stems and branches, which are the

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

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

74

75

76 **2. Material and methods**

77

78 Barraba is a town in the New England region, north of Tamworth in New South Wales (Fig.
79 1A). Plants occur in the marine sediments of the Mandowa Mudstone Formation, in the Devonian
80 part of the Tamworth Belt (Fig. 1B, C). This formation consists of a thick sequence of dark laminated
81 mudstones interbedded with thin layers of whitish siltstones and sandstones (Vickery et al., 2010).
82 The Mandowa Mudstone sites around Barraba have been assigned a Late Famennian age on
83 different lines of evidence detailed in Wright (1988), Vickery et al. (2010), Evreinoff et al. (2017),
84 Champreux et al. (2020). Recent sedimentological work on the Mandowa Mudstone, involving the
85 study of this formation on the Manilla 1:100 000 geological map south of Barraba, suggested that the
86 depositional environment was a distal marine shelf to continental slope (Vickery et al., 2010).

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

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

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

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

108

109

110 **3. Anatomically preserved specimens**

111

112 3.1. Isoëtales, Lycopsidea

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

117

118 3.1.1. *Cymastrobus irvingii*

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

128

129 3.1.2. *Lycaugea edieae*

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

135

136

137 3.2. Iridopteridales

138 A single genus assignable to the Iridopteridales, *Keraphyton*, is recorded at Barraba. It is
139 represented by an anatomically preserved specimen described in Champreux et al. (2020).

140

141 3.2.1. *Keraphyton mawsoniae*

142 *Keraphyton*, and its type-species *K. mawsoniae*, is represented by a single fragment of axis.
143 The specimen is relatively wide (20 mm in its largest dimension) and made of primary tissues only. It
144 is characterized by a highly dissected actinostele consisting of four fundamental ribs connected to a
145 central segment, each fundamental rib dividing unequally (Plate I, 7, 8). Protoxylem strands are
146 mesarch to exarch and occur at the rib tips only. The metaxylem is zonate. It is made of large
147 tracheids measuring up to 140 µm in diameter, bounded externally by 1-2 layers of smaller tracheids
148 (Plate I, 9). The cortex and the ground tissue embedding the stele lack any special cells. The types
149 and number of lateral organs produced per node is uncertain, however the shape of the stele in
150 transverse section suggests that the lateral organs were either decussate or whorled. *K. mawsoniae*
151 is interpreted as a member of the Iridopteridales based on its vascular system, which is actinostelic,
152 entirely primary, with protoxylem strands located at rib tips only (Champreux et al., 2020).

153 *Keraphyton* is unknown outside Barraba.

154

155

156 3.3. Cladoxylopsida

157 The Cladoxylopsida (i.e., the Pseudosporochnales and the informal "non-
158 pseudosporochnalean" group) are represented by several fragments of axes assignable to three taxa.
159 They are characterized by a highly dissected vascular system embedded in a ground tissue. All lack
160 sclereid nests in the cortex, a distinctive character of pseudosporochnalean axes. The species
161 *Polyxylon australe* was the first taxon ever described from Barraba (Chambers & Regan, 1986). The
162 other three taxa, each represented by a single specimen, are new for the locality.

163

164 3.3.1. *Polyxylon australe*

165 *P. australe* is represented by 3 fragments of stems described by Chambers & Regan (1986)
166 and Meyer-Berthaud et al. (2007). These specimens are up to 25 mm in diameter and devoid of any
167 secondary-type of tissue. Branches are produced in whorls of nine or ten separated by internodes
168 exceeding 20 cm in length, which suggests that this taxon may have been non self-supporting,
169 perhaps lianescent.

170 The vascular system of *P. australe* consists of an external ring of radially elongated bundles
171 and of a few smaller central bundles (Plate I, 5). The peripheral bundles fork in their external part and

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

176

177 3.3.2. *Cladoxylon* cf. *taeniatum*

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

180 In transverse section, the vascular system of the stem consists of eleven radially elongated
181 vascular bundles and four to six smaller internal bundles embedded in a ground tissue. All vascular
182 bundles contain tracheids arranged in radial rows that are interpreted as secondary xylem (Pl. II, 2-4).
183 The radially elongated bundles measure 0.3 to 0.7 mm wide and up to 2.8 mm radially. Some are
184 fragmented into two radially aligned bundles of comparable length. They may also divide on their
185 inner side to produce a small internal bundle. The radially elongated bundles show one mesarch
186 protoxylem strand at each extremity (Pl. II, 3). The protoxylem strand located at the external tip is
187 generally associated with a few large, thin-walled cells (Pl. II, 4). Additional protoxylem strands occur
188 in the central part of the longest bundles (Pl. II, 2). The small internal vascular bundles show one or
189 two centrarch protoxylem strands. Protoxylem tracheids are 18-30 μm wide. There is no conspicuous
190 zonation of the metaxylem tracheids, which are polygonal and up to 80 μm wide (mean diameter =
191 53 μm) in transverse section. The secondary xylem is relatively thick, up to 8 cells broad and appears
192 slightly excentric in some bundles (Pl. II, 3). Secondary xylem tracheids tend to be rectangular and
193 have dimensions comparable to those of the primary xylem tracheids. They range from 40 to 78 μm
194 in diameter (mean = 59 μm). Each vascular bundle is separated from the ground tissue by a layer of
195 cells that are generally less compressed than the neighbouring cells. They range from 55 to 75 μm in
196 width and may correspond to an endodermis (Pl. II, 3, 4). The ground tissue is an homogeneous
197 parenchyma made of thin-walled cells that are often compressed and range from 45 to 100 μm in
198 diameter. This tissue does not show any special features like sclereid nests or sclerenchyma plates in
199 its most external part.

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

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

208

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

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

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

228 The closest taxon to specimen BA8 is *Cladoxylon taeniatum* from the Tournaisian locality of
229 Saalfeld, Germany (Unger, 1856; Solms-Laubach, 1896; Bertrand, 1935). A second species from
230 Saalfeld, designated as *Cladoxylon dubium* by Solms-Laubach (1896), has been transferred to *C.*
231 *taeniatum* and named *C. taeniatum* var. *dubium* by Bertrand (1935). Axes referred to as *C. cf.*
232 *taeniatum* have also been described from a Tournaisian locality of Montagne Noire, France (Galtier,
233 1970; Scott et al., 1984). The specimens representing *C. taeniatum* var. *dubium* and *C. cf. taeniatum*
234 are smaller than the *C. taeniatum* type-specimen and than specimen BA8.

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

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

246

247 3.3.3. *Cladoxylon radiatum*

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

251 In transverse section, the stele consists of thirteen radially elongated vascular bundles, and 1-
252 4 small internal bundles embedded in a ground tissue (Pl. II, 7). U- or V-shaped bundles are formed
253 when neighbouring elongated bundles interconnect at their inner extremity (Pl. II, 5). Some
254 elongated bundles divide at their inner end and produce internal bundles. No radially elongated
255 bundle crosses the stele from side to side. The radially elongated bundles measure 0.2 to 0.35 mm
256 wide and up to 3 mm radially. They show two mesarch protoxylem strand sometimes associated with
257 thin-walled cells, one at each end (Pl. II, 6). Additional protoxylem strands are found in the longest
258 bundles. The small internal vascular bundles show at least one centrarch protoxylem strand. There is
259 no conspicuous zonation of the metaxylem tracheids, which are up to 45 µm wide in transverse
260 section. The phloem is represented by a zone of badly preserved cells, which surrounds the
261 metaxylem, and is especially conspicuous in the inner bundles. On the other hand, each vascular
262 bundle is bounded externally by a prominent layer of rectangular thick-walled cells (Pl. II, 6).
263 Thickenings are often greater on the tangential walls. From the position of this layer and the
264 distinctive shape of its cells, and despite the fact that the radial walls are not necessarily thicker, we
265 interpret it as an endoderm. The cells of the ground tissue range from 45 to 65 µm wide. This tissue
266 is homogeneous and does not show any special cells nor features like sclereid nests in the outermost
267 zones.

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

273

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

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

282

283 3.3.4. *Hierogramma* sp.

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

287 In transverse section, the vascular system consists of more than fifteen tangentially
288 elongated strands of different sizes embedded in a ground tissue. The strands are aligned in three
289 parallel rows but it is uncertain to what extent this arrangement results from the deformation of the
290 specimen. The strands on one face are lobate on their external surface (Pl. III, 2). The protoxylem is
291 exarch and solid (Pl. III, 3). The metaxylem tracheids are large, ranging from 30 to 120 µm in
292 diameter. The primary xylem is surrounded by a tissue, presumably the phloem, which consists of
293 about 10 rows of small cells enclosing a layer of much larger elements (Pl. III, 3). The small cells are
294 polygonal and measure 15-40 µm in diameter. The large elements are 60-80 µm wide radially and 25-
295 45 µm wide tangentially. They may represent sieve cells.

296 The ground tissue, which is made of thin-walled cells, is highly compressed in the center, a
297 little less in a 1.5-2 mm thick zone external to the vascular strands. Cells in this tissue are up to 130
298 µm wide. Isolated thin-walled cells of larger dimensions (up to 200 µm wide) and without any
299 deformation are scattered throughout the ground tissue (Pl. III, 2). The surrounding cortex is 1.25
300 mm thick. Its small thick-walled cells have retained their polygonal shape. The largest ones are up to
301 90 µm in the vicinity of the ground tissue. They decrease to a width of 45 µm in the outermost
302 cortical layers.

303

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

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

319

320

321 3.4. Archaeopteridales, Progymnospermopsida

322

323 3.4.1. *Callixylon* sp.

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

331

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

340

341

342 3.5. Pteridospermales, Spermatophytes

343

344 3.5.1. *Kalymma grandis*

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

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

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

361 The sparganum cortex is 550 to 780 μm thick (Pl. III, 5). It is thicker on the convex part (Pl. III,
362 4). The individual sclerenchyma bands are 170 μm wide. They range from 270 to 470 μm radially in
363 the thinnest part of the cortex, and are up to 600 μm in the thickest part where they eventually split
364 in two. Sclerenchyma cells are 16 to 40 μm wide, most around 25-30 μm . The parenchyma cells
365 between the sclerenchyma plates are larger, from 25 to 75 μm in diameter, a large number around
366 50 μm . The subepidermal cells external to the sparganum decrease in diameter, from 45 μm near the
367 sclerenchyma plates to 25 μm outside.

368
369 **Identification** - Specimen BA1 is assignable to *Kalymma* (Unger) Braun & Wilde (Unger, 1856; Braun
370 & Wilde, 2001), a genus corresponding to anatomically preserved petioles and rachises of
371 calamopityacean affinities (Sebby & Matten, 1969). Such petioles and rachises are characterized by a
372 subepidermal tissue of sparganum-type. The vascular bundles, which tend to be separate in the
373 proximal parts of *Kalymma* petioles and connected in more distal portions of the fronds, are
374 arranged in a ring or a C-shaped configuration within a parenchymatous tissue. *Kalymma* petioles
375 may form a wide angle with their parent axis and are often broken at their insertion level (Long,
376 1964; Galtier, 1974). The Barraba specimen, which is preserved on one side only and has a majority
377 of separate vascular bundles, may correspond to the proximal part of a petiole, close to the level of
378 attachment to the stem from which it was torn. In this case, the thickened part of the sparganum
379 would be on the abaxial side, a feature probably involved in the support of the frond.

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

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

401

402

403 **4. Adpression specimens**

404

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

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

431

432

433 5. Miospores

434

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

443

444

445 6. Discussion

446

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

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

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

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

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

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

484 from the New Albany Shale in eastern USA) and the European terranes (e.g., the floras from Saalfeld
485 in Germany, and Montagne Noire in southern France). It is with the New Albany Shale floras that the
486 Barraba plant assemblage shares the greatest number of similar taxa. The mid-tournaisian floras
487 from Saalfeld and Montagne Noire are the youngest and are preserved in marine sediments like the
488 Barraba specimens. They have *Cladoxylon*, *Hierogramma* and *Kalymma* in common with the Barraba
489 plant assemblage, but their lycopsids are different and they do not show any archaeopteridalean
490 progymnosperms (Galtier, 1970; Meyer-Berthaud, 1984). In Ireland, three plant localities dated of
491 the latest Famennian have been recorded, Kiltorcan, Ballyheigue and Hook Head (Jarvis, 1990). They
492 represent floodplain and fluviatile environments (Matten, 1989). Apart from *Archaeopteris* the
493 adpressions at Kiltorcan, which include lycopsid remains of *Cyclostigma/Jurinodendron* and the
494 platyspermic seed *Spermolithus*, are unlike any taxa from Barraba (Holland, 1981; Chaloner et al.,
495 1977). Ballyheigue yielded anatomically preserved specimens, all assignable to the seed plants
496 (Matten et al., 1984). The only taxon resembling a plant from Barraba is the lycopsid *Wexfordia*
497 *hookense*, from Hook Head, which has been compared with *Lycaugea edieae* (Matten, 1989; Meyer-
498 Berthaud et al., 2021). The late Famennian to early Tournaisian floras from the New Albany Shale
499 were recovered from marine sediments. They have four genera in common with the Barraba plant
500 assemblage, *Polyxylon*, *Hierogramma*, *Callixylon* and *Kalymma* (Read & Campbell, 1939; Hoskins &
501 Cross, 1952). *Cladoxylon* is not reported in the New Albany Shale but *Hierogramma* suggests its
502 occurrence. In addition, resemblances were noted between the lycopsids from Barraba and two taxa
503 from the New Albany Shale, *Lycaugea* and the Cichan & Beck (1987)'s specimen from Kentucky on
504 one hand, *Cymastrobis* and *Flemingites noei*, also from Kentucky (Mathews, 1940) on the other hand
505 (Evreinoff et al., 2017; Meyer-Berthaud et al., 2021). The Barraba plant assemblage differs from the
506 Famennian floras of South China (Xiong et al., 2013) with which it shares only the cosmopolitan
507 genera *Callixylon* and *Leptophloeum*, and, possibly, a spermatophyte with delicate fronds of the
508 *Cosmosperma*-type. These statements are consistent with earlier considerations of a cosmopolitan
509 character of the Late Devonian floras from Australia, tempered by the evidence of specific taxa
510 suggesting some level of provinciality at the genus or species level (Hill et al. 1999; Playford in Talent
511 et al., 2000). They are also consistent with a palaeogeographic connection between Gondwana and
512 Southern Laurussia during the late Famennian whereas geographic barriers may have prevented
513 extensive floral exchanges between the eastern part of Gondwana and South China at this time
514 (Torsvik & Cocks, 2013).

515

516

517 **7. Conclusion**

518

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

541

542

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561

562

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728

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730

731 **TABLE LEGEND**

732 Table 1. List of specimens described in this paper.

733

734

735 **FIGURE LEGEND**

736

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

742

743

744 **PLATE LEGENDS**

745

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

748 1-2. *Cymastrobis irvingii*, holotype NMVP 161998. 1. Cone in external view; 2. Detail of the cone axis
749 showing the undulated border of the primary xylem and emission of a sporophyll trace.

750 3-4. *Lycaugea edieae*, holotype NMVP 161999.0. 3. General view of axis showing medullated stele,
751 three-zoned cortex and small leaf bases at periphery; 4. Detail showing the smooth border of the
752 primary xylem and sporophyll traces in the inner cortex.

753 5-6. *Polyxylon australe*, F65557. 5. General view of axis showing the ring of radially elongated
754 vascular bundles; 6. Detail of the dichotomizing extremity of a vascular bundle.

755 7-9. *Keraphyton mawsoniae*, holotype MMF44986. 7. General view of axis showing the actinostelic
756 vascular system, and cortex on the bottom side; 8. Detail of a dividing rib; 9. Detail of the central part
757 of the stele.

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

759

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

762 1-4. *Cladoxylon cf. taeniatum*, specimen BA8. 1. General view of axis; 2. Detail of radially elongated
763 bundles producing traces in two rows; 3. Detail of radially elongated bundles and ground tissue; 4.
764 Detail of two radially elongated bundles showing the protoxylem strands associated with a lacuna in
765 the primary xylem, and the surrounding secondary xylem.

766 5-8. *Cladoxylon radiatum*, specimen BA4. 5. General view of axis; 6. Detail of two radially elongated
767 bundles surrounded by a conspicuous layer of endodermis cells, and showing the protoxylem strands
768 associated with a lacuna in the primary xylem; 7. Detail of radially elongated bundles and a row of
769 elongated traces; 8. Detail of traces in two rows ; bt1 and bt2 are successive branch traces produced
770 by a radially elongated bundle.

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

772

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

775 1-3. *Hierogramma sp.*, specimen BA2. 1. General view; 2. Detail of a lobate vascular strand; 3. Detail
776 of a vascular strand showing the primary xylem and surrounding phloem with a row of large cells
777 between two layers of smaller elements.

778 4-6. *Kalymma grandis*, specimen BA1. 4. General view; 5. Detail showing two missing vascular
779 bundles embedded in a ground tissue, and the sparganium cortex on the outside; 6. Two vascular
780 bundles after separation, each one with two protoxylem strands.

781 7-9. *Callixylon sp.*, specimen BA10, radial MEB views. 7. Radial walls of tracheids showing multiseriate
782 bordered pits in groups; 8. Detail of a group of bordered pits showing slit-like openings; 9. detail of a
783 ray showing four rows of parenchyma cells.

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

785

786 **Plate 4.** Specimens preserved as adpressions.

787 1-2. *Leptophloeum* axes. 1. Dichotomous axis showing different levels of decortication, locality 1; 2.
788 Specimen showing leaf bases that are as wide as high, locality 2.

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

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

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

792 6-7. Frond of putative seed plant affinities, locality 1. 6. Proximal part showing a petiole branching
793 dichotomously, producing two primary rachises; 7. Primary rachis at top of previous figure showing
794 departure of three secondary rachises arranged alternately at arrows.

795 8. Part and counterpart of a putative seed borne on a long, narrow stalk, locality 2.

796

797 **Plate 5.** Miospores.

798 Specimens are arranged according to sample number and England finders coordinates.

799 1. cf. *Criticavatisporites dispersa* González, Playford and Moreno, 2005, 77167, 18M194, B15/0.

800 2. *Corbulispora* sp., 18B192, BAR1, M18/0.

801 3. Unidentified apiculate monolete spore, 77167, 18M194, B15/0.

802 4. cf. *Tumulispora rarituberculata* (Luber) Potonie, 1966, 77167, 18M194, E15/3.

803 5, 6. *Retispora lepidophyta* (Kedo) Playford 1976, 77167, 18M194, F31/0; 18B192, 30/3.

804 7. *Verrucosisporites congestus* Playford 1964, 77167, 18M194, L45/2.

805 8, 9. *Verrucosisporites nitidus* Playford 1964, 19B192 BAR1, C26/1 ; Q21/0.

806

807

FIG.1

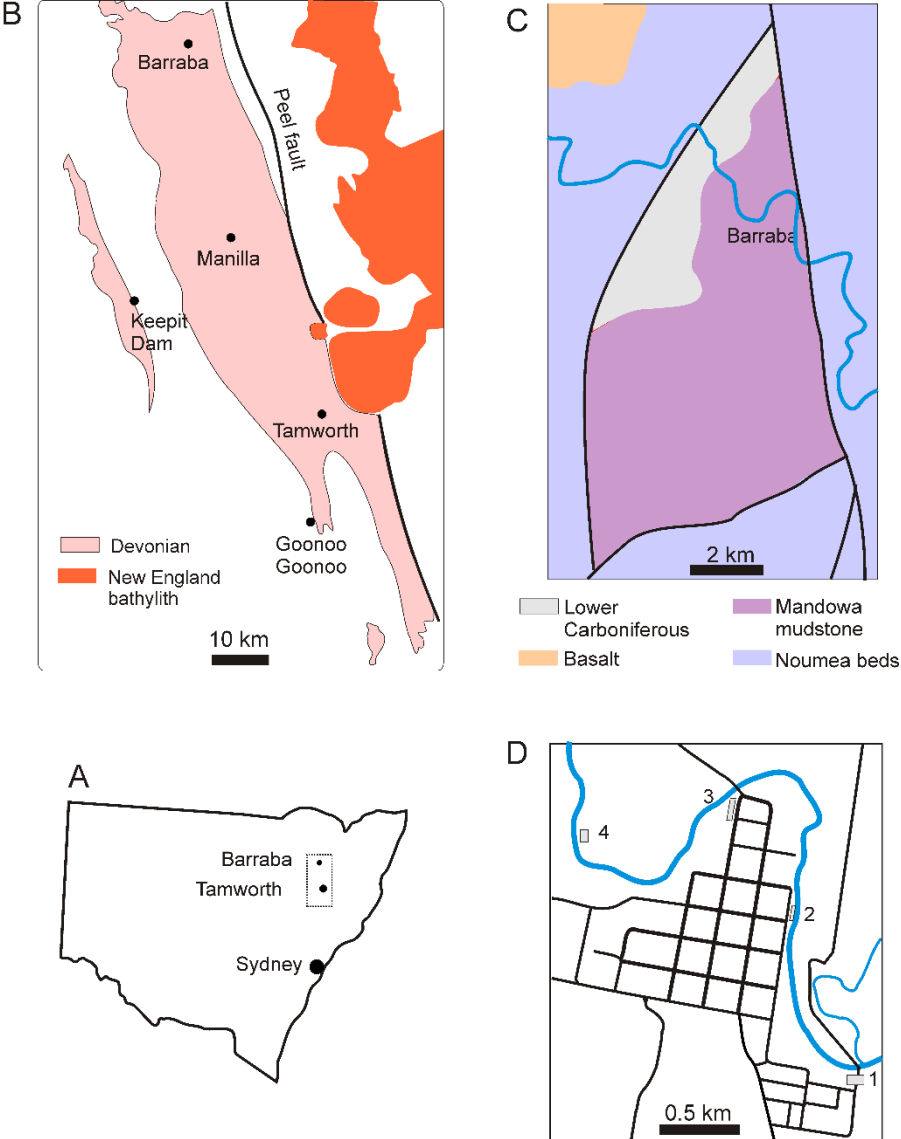


PLATE 1

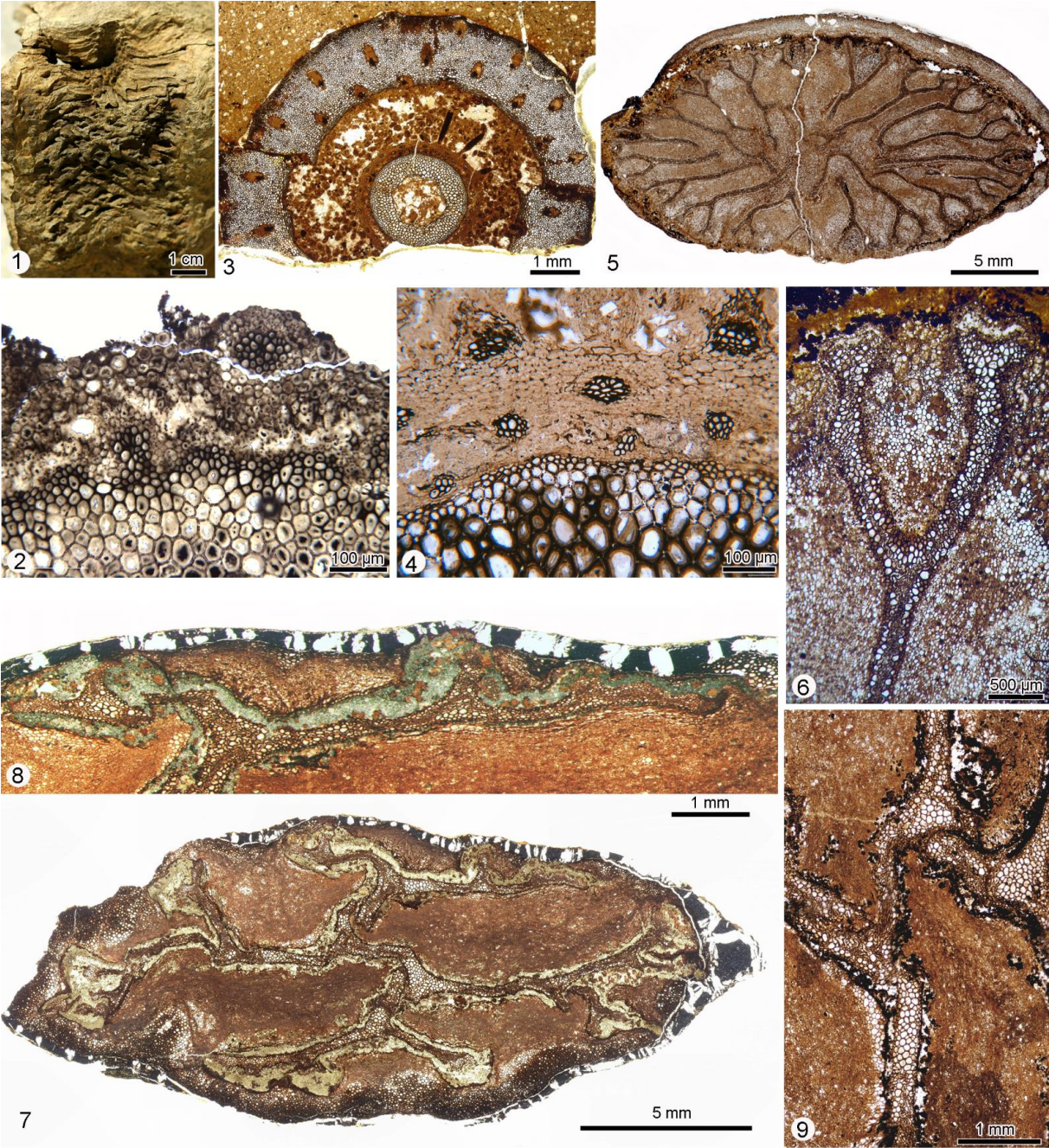


PLATE 2



PLATE 3

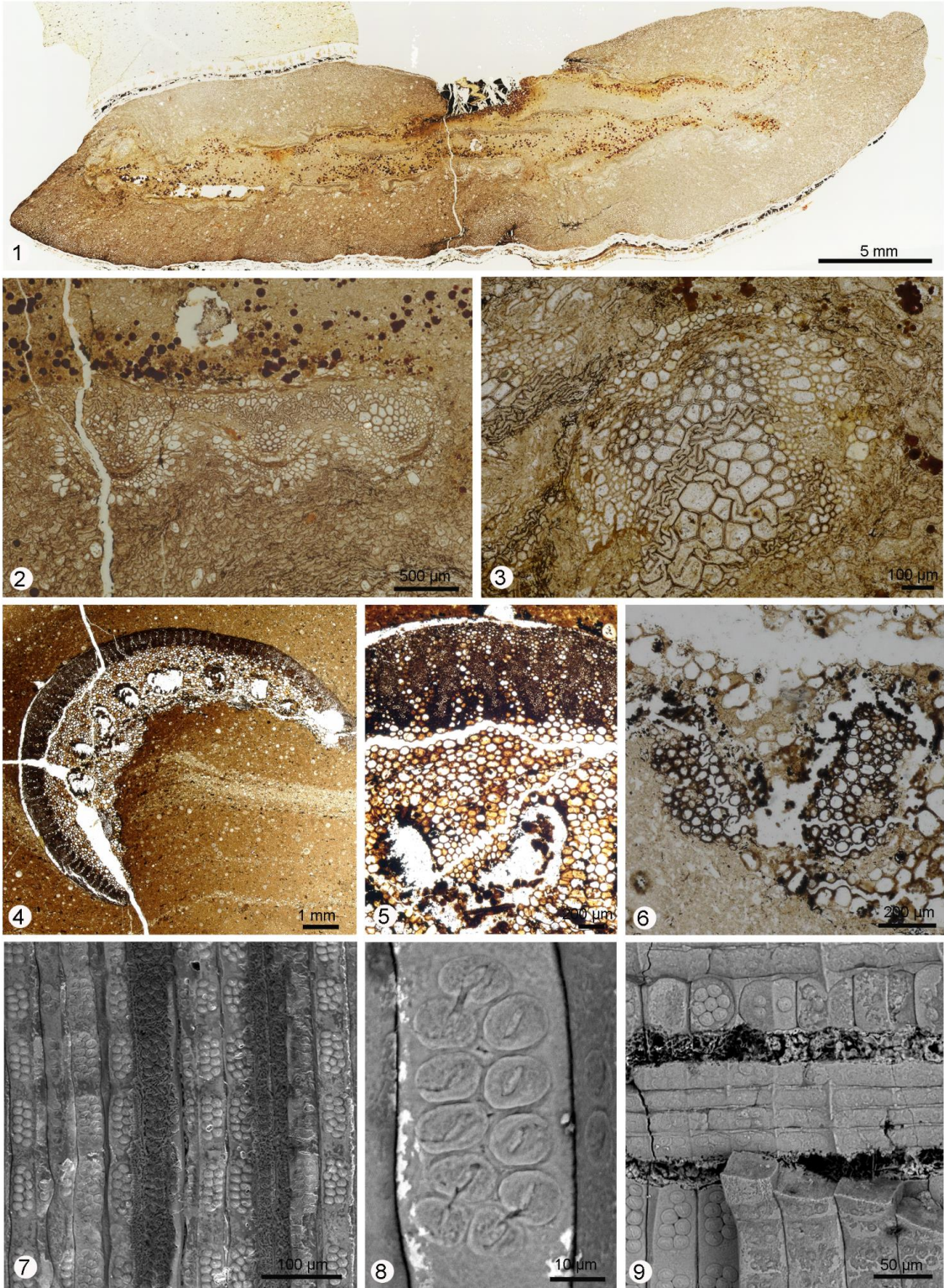


PLATE 4

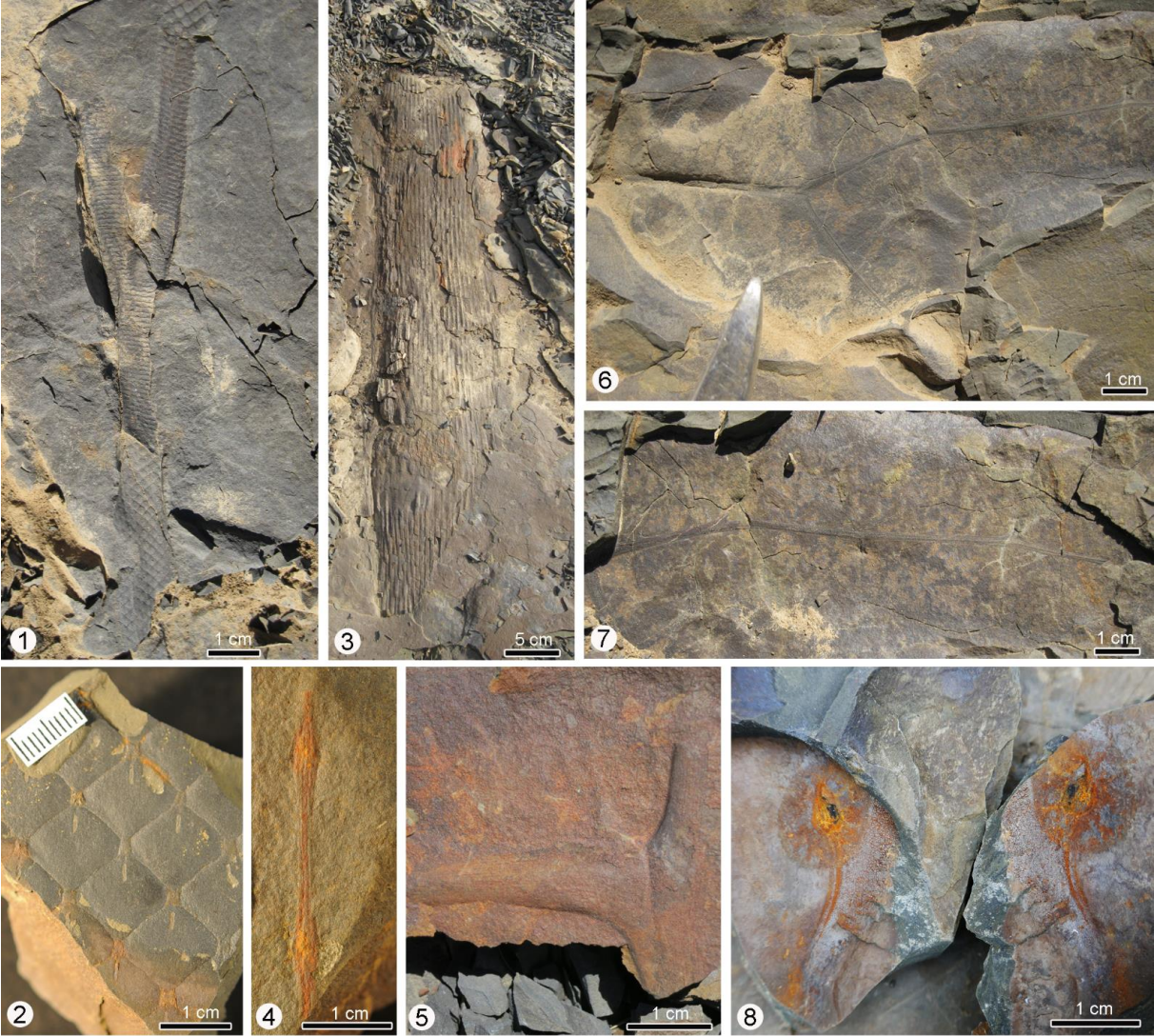


PLATE 5

