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1 Promoting a standardized description of fossil tracheidoxyls

2

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4

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13

14 Abstract: The palaeoxylology of coniferous woods has progressed considerably since
15 Kräusel's last (incomplete) synthesis in 1949. Nomenclatural practice has slowly purged itself
16 of the diagnostic use of etymology. The use of certain new words or phrases has become
17 essential, while other words have been subject to significant semantic drift or unjustified
18 omission. The interest of secondary characters was highlighted. Ways of describing have also
19 evolved, sometimes in divergent ways. The list of characters (and states) published by the
20 International Association of Wood Anatomists in 2004 represents a fundamental step towards
21 a standardization of practices. However, it does not take into account some of the
22 particularities of palaeoxylology. Here we propose: 1) a plea that etymology should definitely
23 no longer be considered diagnostic; 2) a standardised format for the description of fossil
24 tracheidoxyls; 3) an illustrated glossary of certain terms specific to palaeoxylology.

25

26 Key-words: fossil wood; homoxyulous wood; taxonomy; xylology.

27

28

29 1 Introduction

30

31 Since the pioneering works of fossil softwood taxonomy (Gothan, 1905; Jeffrey, 1905;
32 Kräusel, 1919; Torrey, 1923; Slyper, 1933) there have been few updates (Kräusel, 1949;
33 Vogellehner, 1967, 1968; Philippe and Bamford, 2008), despite significant contemporaneous
34 works on extant conifer woods (Pool, 1929; Greguss, 1955; Jacquot, 1955; Chavchavadze,

35 1979; Barefoot and Hankins, 1982; Garcia Esteban et al., 2002). Modern authors do not
36 always go back to basics, and for their works rely only on more recent publications. This
37 logically led to a divergence in the semantics of the words used to describe softwoods. All the
38 more as etymology-based hypotheses are still too often used in both the nomenclature and the
39 taxonomy of these woods. In addition, as knowledge progresses, new words have been
40 proposed to avoid long locutions: for example “tracheidoxyl” instead of “detached portion of
41 wood characteristically composed of tracheids with only a minor proportion of other tissues”
42 (Creber, 1972), or “oculipore” for “half-bordered cross-field pit” (Torrey, 1923). As there has
43 been no recent review of how to describe fossil softwood, these words are rejected by most
44 editors as jargon, and thus are condemned to idiosyncratic uses, despite their undeniable
45 practicality. Finally, more importantly, the completeness of published descriptions for fossil
46 woods differ greatly, with too much variation in attention paid to traits considered secondary.
47 A formalization seems desirable.

48 After the IAWA’s glossary (1964), the “Inside Wood” project was a huge step forward for
49 hardwoods in standardizing what xylological vocabulary means and how woods are to be
50 described (InsideWood, 2004; Wheeler, 2011). Similarly, after Slyper’s illustrated key (1933)
51 and Phillips’ card system (1941), the IAWA list of microscopic features for softwood
52 identification (Richter et al., 2004) was also such a step. Immo Heinz’s thesis (2004), though
53 still unpublished, is also a significant contribution to the study of extant softwoods. These
54 works do not tackle, however, some of the vocabulary that is commonly used for fossil
55 softwoods (e.g. podocarpoid crossfield pit, or mixed type of radial pitting). Later some
56 authors tried to fill some of these gaps (e.g. García Esteban et al., 2002, 2004; Merlotti, 2011;
57 Pujana and Ruiz, 2017; Pujana et al., 2016).

58 Our experiences, as authors and as editors, force us to note that a synthesis is necessary
59 regarding the vocabulary and the way of describing fossil softwoods. Here we propose: 1) a
60 plea for the definitive abandonment of any etymologically based implication in the taxonomy
61 of fossil woods; 2) a standardized format for described fossil tracheidoxyls, together with
62 warnings about the tricks played by fossilization that we seem to encounter most often in
63 contemporary palaeoxylological literature; 3) an illustrated glossary of some terms commonly
64 used for softwood palaeoxylology, including three new words to replace longer locutions.

65

66

67 2 Fossil wood nomenclature and etymology

68

69 Fossil wood anatomy was illustrated as early as 1665 (Hooke, 1665), but was first studied in
70 the 1830's (Nicol, 1831, 1834). As for softwoods it was not before Eßner (1886), and
71 specially Gothan's thesis (1905), that cross-field pitting was evidenced to be a key taxonomic
72 feature. Subsequently, numerous authors have proposed founding taxonomic syntheses for
73 fossil softwood (e.g. Jeffrey, 1905; Kräusel, 1920a and b, 1949; Eckhold, 1923; Seward,
74 1919). All of these studies have largely used etymology at two levels (Philippe and Bamford,
75 2008), ignoring the establishment of nomenclatural rules when they were first promulgated
76 (known as the Vienna rules, 1905).

77 First in the naming of genera, assigning fossil wood samples to genera not on the basis of
78 diagnoses, but according to which extant genus they thought it was most similar to (see
79 Kräusel, 1917: 306-307 and 1918: 129-130). A softwood resembling the wood of a
80 *Podocarpus* (or of a Podocarpaceae, not always clear) had to be named *Podocarpoxylon* (see
81 e.g. Tuzson, 1911; Kräusel, 1913; Greguss, 1967). It is obvious that this method, largely
82 based on fixist views and idiosyncratic similarity hypotheses, is simplistic. In the minds of
83 these authors, the fossil wood genera not being "natural" ones, escaped the rigor of
84 nomenclatural laws and their names could therefore mnemonically formalise their supposed
85 affinities through etymology. Using mnemonics is not a nomenclatural problem but a
86 hypothesis cannot replace a diagnosis and the etymology cannot be diagnostic ("The purpose
87 of giving a name to a taxonomic group is not to indicate its characters", ICN preamble 1,
88 Turland et al., 2018). The progression of wood anatomy, by documenting the xylological
89 variability of several extant genera (see e.g. Bailey, 1933; Bailey and Faull, 1934), evidenced
90 that this approach was not tenable. However, this was not usually admitted before the 1970's,
91 and even much later some authors still explicitly used a taxonomical hypothesis and then
92 etymology to name a fossil wood (Greguss, 1967). Quite often this approach is used still now,
93 more or less conscientiously. The etymology may have played a role in the connection that
94 has sometimes been made between *Brachyphyllum* Brongniart and *Brachyoxylon* Hollick &
95 Jeffrey together, although there is no evidence of an exclusive relationship (Lemoigne, 1968;
96 Greppi, 2021).

97 Second is the understanding of the vocabulary used for descriptions. Although conscientious
98 authors have published definitions of the terms they used (e.g. Kräusel, 1920b; Slyper, 1933;
99 Vogellehner, 1967, 1968), and more rarely illustrated them, several words have been used
100 with no definition, or with no reference to an original use, i.e. only on the basis of etymology.
101 One of the foremost examples is the use of the term podocarpoid (Philippe and Bamford,
102 2008), which was originally used for a cross-field pit with a narrow linear oblique pore

103 (Gothan, 1905), but subsequently as a large round narrowly bordered cross-field pit (Müller-
104 Stoll and Schultze-Motel, 1990). “Podocarpoid” does not mean “like the one encountered in
105 *Podocarpus* wood” (where cross-field pits are diversified), but rather in fitting with a
106 description (as given first by Gothan, 1905).

107 This unjustified use of etymological diagnostics at two levels is characteristic of what was
108 referred to as “*etymological naming*” (Philippe and Bamford, 2008). This has long prevented
109 a homogenisation of nomenclatural approaches, but instead induced a plethoric synonymy,
110 and made syntheses, whether systematic, phylogenetic or biogeographic, extremely difficult.
111 Moreover, as Latin and Greek are less and less part of common education, etymological
112 implications are nowadays more often misunderstood.

113

114

115 3 Fossil tracheidoxyl description

116

117 A definition is given in the subsequent glossary for terms marked with an asterisk.

118 Here we propose a template for the description of fossil tracheidoxyls* (Plate I, 1), i.e.

119 softwoods made of tracheids, with only a minor proportion of other cell types. Manoxylic*

120 woods (Plate I, 2) consist of a large proportion of axial parenchyma and are not concerned

121 here, tracheidoxyls being typically pycnoxylic* (Plate I, 1). Homoxylic angiosperms might

122 have a wood superficially similar to softwoods, but apart from some rare exceptions (Philippe

123 et al., 2010), are usually easy to distinguish.

124 Referring to a template has the advantage of making the absence of a character more explicit.

125 Thus the descriptions can become more concise, avoiding statements like "axial parenchyma

126 not observed". It also makes it easier to access information as its position in the text is

127 standardised.

128 Xylological descriptions of softwoods are already standardised to a certain extent, since the

129 majority of authors describe the woods in a sequential way, starting with the cross-section,

130 then the tangential and radial axial sections. This way, however, implies repetition, and the

131 dispersion of characters specific to each cell type. Here we propose a template where, after

132 some general lay out features, each wood cell type is described independently by integrating

133 observations made in each of the section plans. Heteroxylic woods are usually described in

134 this way today.

135 The description is limited to microscopic features. Macroscopic features are also of interest, in

136 particular axis diameter (measured or estimated from ring curvature), as several wood features

137 are a function of radius: ray height; tracheid width and hence pit seriation; resin canal density;
138 etc.

139 Continuously variable parameters, such as the diameter of pits in μm , are of undeniable
140 interest for the diagnosis of today's woods (Richter et al., 2004). Their interest for fossil
141 woods is more debatable. The values they take are indeed strongly influenced by the type of
142 fossilization (Rößler et al., 2021). During charcoalification the diameter of the pits can
143 decrease by more than 30%, while the sideritization can increase it by almost 20% (Philippe,
144 1995). Most fossilization processes induce allometric transformations. Quantification is
145 desirable. All too often, however, quantification is practiced as an end in itself, which can border on
146 scientism, and does not encourage perspective taking

147 Fossilization often plays tricks that have often deceived palaeoxylogists, in particular
148 steinkerne preservation, pore broadening and false spirals. By steinkerne preservation, which
149 is very common, especially in silicified woods, the areolate pit inner chamber is maintained,
150 more or less completely, while its real rim is indistinct (Bamford et al., 2016). This type of
151 preservation was known to Gothan (1905), who wrote of “*Steinkerne*” preservation (literally
152 “stone kernel”). When this occurs, araucarian* pitting displays small rounded and spaced
153 casts instead of larger contiguous and deformed pits and can be confused with abietinean*
154 pitting. Usually two criteria can be used to avoid misidentification of a uniseriate araucarian*
155 radial pitting preserved as Steinkerne as opposed to abietinean* radial pitting: first, the areole
156 is usually at least faintly marked, either by a paler crown around the pore, or by a darker line
157 at the rim of the areolate pit chamber; secondly, in araucarian* radial pitting the spacing
158 between pit pores is usually constant, which is rare in abietinean* pitting (Bamford et al.,
159 2016). Steinkerne preservation should be suspected anytime pits look relatively small on the
160 radial wall.

161 Thinon (1994) and Gerards et al. (2007) have shown that by charcoalification pit pores often
162 significantly widen. This has a particular impact on the characterization of cross-field pits, for
163 which the ratio between pore and pit outline is much used. It is possible that other types of
164 fossilization allometrically alter the microscopic characters of the woods. Indentures usually
165 shrink during the taphonomic process (Thinon, 1994), while microbial attack deeply modifies
166 most cell walls (Anagnost, 1998; Schweingruber and Börner, 2018).

167 There are multiple types of structures that are known to have been confused with helical
168 thickenings (Philippe et al., 2019): tracheid wall checking by compression wood; oblique
169 furrows at the bottom of which a pit pore is located, also by compression wood; zoned
170 patterns caused by discontinuous crystal growth; crystal cleavage planes by polyblastic

171 mineralization (Buurman, 1972); tunnelling by bacteria or fungi; shrinkage cracks induced by
172 wood diagenesis; microbial erosion of the tracheid wall that emphasizes the S2 microfibrillar
173 patterns.

174 The saproxylic process can begin even before the wood is entrained in the taphonomic
175 process, when it is still inside a living tree. Saproxylicism is of enormous ecological
176 importance, and it leaves visible traces in the majority of fossil woods. Traces of arthropods
177 or bivalves have been mentioned or studied for a long time, but it is only recently that the
178 authors have begun to describe the effects of bacterial and fungal attacks (e.g. Stubblefield &
179 Taylor, 1986, Scaramuzza dos Santos et al., 2020). As these attacks often modify the
180 appearance of the wood, it is important to describe them before coming to the description of
181 the wood cells. Such features are: occurrence of pocket rots; occurrence and type of hyphae
182 (septate or not, branched or not); occurrence and type of propagules or spores; presence of
183 dark substance; loss or degradation of a more or less important parts of cell walls (middle
184 lamella, primary wall, secondary wall); bacterial slime within tracheid lumen.

185

186 Below are lists of the character states for each of the features that should be looked for to
187 assist with capturing all the important features for describing and identifying fossil softwood.
188 The numbers between brackets refer to the IAWA's softwood features coding (Richter et al.,
189 2004). Intertracheary pitting types (abietinean* (Plate III, 1), araucarian* (Plate III, 2),
190 brachyoxylean* (Plate III, 3 & 4), shimakurean* (Plate III, 5), xenoxylean* (Plate III, 6)) are
191 not included in this template insofar as the determination of this type is already partly
192 interpretative, and therefore belongs to a discussion.

193

194 General cell layout

195 tracheidoxyl*; ring curvature; occurrence of true (complete and asymmetrical) growth-rings
196 (present [40], indistinct or absent [41], present but narrow - for respectively, the "A", "B" and
197 "C" types, the "O" type, and the "D" and "E" (Plate I, 3 & 4) types according to the Creber
198 and Chaloner's nomenclature (1984); type of transition from the early- to the late-wood when
199 developed [42-43]; proportion of early-wood to late-wood; occurrence of false rings* (Plate I,
200 5 & 6), either symmetrical or incomplete; occurrence of intercellular spaces [53]; relative
201 position of the tracheid in relation to its tangential neighbours (opposite or alternate); other
202 features (e.g. late wood much developed, circular shape of tracheid cross-section, spiral
203 cracks in axial tracheid walls, wavy rings, branch traces, traumatic areas, fleck marks, etc.).

204 Rays homogenous (including only parenchyma cells) or heterogeneous (occurrence beside
205 normal uniseriate rays of fusiform rays and/or of rays with a radial resin canal); rays
206 homocellular (including one type of cell only) or heterocellular (rays including several cell
207 types and/or cell size as in the case of broader marginal cells or of ray tracheid) (Plate II, 1 &
208 2); for each type of ray seriation (uniseriate [107], locally biseriate [108], multiseriate (Plate
209 II, 3) and ray height in number of cells (minimum, average, maximum) [102-106] and/or in
210 μm [101]; occurrence of intercellular spaces between ray cells (Plate I, 7).

211

212 Axial tracheids

213 Cross-section shape (circular (Plate II, 4) or polygonal (Plate II, 5); relative tracheid wall
214 thickness (relative to the lumen, in early and late wood [54-55], tracheid size (diameter and
215 length [49-52], if measurable); variability of tracheid diameters along radial rows.
216 Shape (round, elliptic, obround, xenoxylean*(Plate III, 6), scalariform (Plate III, 7)), size and
217 disposition (contiguous or distant) of intertracheary areolated pits on the radial wall of
218 tracheids; their seriation (uni- [44], bi- or multi-seriate [45] and their relative position in the
219 earlywood when bi- (multi-)seriate (alternate [47], opposite [46], in distinct bands (Plate III,
220 8) or clustered (Plate III, 9); variation of radial pitting through the growth-ring; occurrence of
221 Sanio's rims* (Plate IV, 1 & 2); torus [56] and margo characteristics (round, scalloped [57],
222 extensions [58]); radial pits peculiar features (such as notched borders [59], other).
223 Pits on the tangential walls of tracheids (Plate IV, 3), their size, their disposition and their
224 distribution in the ring.
225 Occurrence [61] and characteristics (localization within the ring [62-64], single [65] or
226 grouped [66], more or less spaced [67-68], angle from the horizontal) of tertiary thickenings
227 (spirals, callitroid [71], others) or other cell wall ornamentation (wart-like layers [60]).
228 Other features like resiniferous [48] or mineral contents (Plate IV, 4); occurrence of storeyed
229 or crooked (club-shaped) tips (Plate IV, 5), tyloses (Plate IV, 6 & 7), septae (Plate IV, 8), Bars
230 of Sanio* (Plate IV, 9), etc.

231

232 Axial parenchyma (epithelial and subsidiary cells of intercellular canals excluded).

233 Occurrence [72]; distribution through the ring (diffuse [73], tangentially zonate[74],
234 marginal[75]); association with rays; inflated or not; transverse walls, thin or thick, nodular
235 [77-78] or smooth [76]; pitting of the axial parenchyma, on normal walls and in cross-fields;
236 including crystals [118, 123] or not, type of crystals (prismatic [119], druses [120], other
237 forms [121]); resiniferous or not.

238

239 Ray parenchyma: shape in cross-section; cell length; angle of transverse walls; thickness of
240 walls; occurrence of pits (unpitted [85], distinctly pitted [86], abietineentüpfelung* (Plate I, 7;
241 Plate V, 1), juniperustüpfelung*(Plate V, 2 & 3) in ray cell end walls; occurrence of pits
242 (unpitted [87], distinctly pitted [88]) in horizontal walls; occurrence of indentures [89];
243 type(s) of crossfield [90-95] (Plate V, 6) semi-areolated (cupressoid*, podocarpoid*,
244 taxodioid*) or unbordered (oopore*, circopore* (Plate V, 8), phyllocladoid*(Plate V, 7)
245 oopore) pits in the early wood cross-fields; number (minimum, average, maximum) [96-100]
246 and disposition (spaced, in lines, grouped, contiguous, araucarioid*, circoporoid*,
247 dacrydioid* (Plate V, 8), glyptostroboid*, pinoid*) of crossfield pits in the early wood;
248 variation of crossfield pitting through the growth ring; presence [118, 122] and type of
249 crystals (prismatic [119], druses [120], other forms [121]).

250

251 Ray tracheids: occurrence [79-80]; size; wall thickness, characteristic (smooth [81], dentate
252 [82], reticulate [83]) and pitting (unpitted or distinctly pitted, pit borders angular or with
253 dentate thickenings [84]); tertiary thickenings (present [69-70] or absent).

254

255 Axial and/or radial resin-canals: occurrence (normal [109-110] or traumatic [111] or absent),
256 grouping and position within the ring; size (tangential and radial diameter delimited by
257 epithelial cells diameter [112-115]); traumatic or not, their distribution within the ring; feature
258 of the resin-canal lining epithelial cells (thick [116] or thin-walled [117]); presence [124] and
259 type of crystals (prismatic [119], druses [120], other forms [121]).

260

261 Idioblasts (Plate V, 4 & 5): occurrence; size; distribution.

262

263

264 4 Glossary

265

266 Only those terms commonly used for tracheidoxyls but which are not illustrated in IAWA's
267 list (Richter et al., 2004) are treated. The reader is warned that the definitions given here are
268 based on the first time the term was used, and that subsequent semantic shifts have
269 occasionally occurred, which are not taken into account. For each entry the author who first
270 used the term for fossil wood is quoted. Some old literature might have been overlooked,
271 however the term in the indicated reference is used according to its "original" meaning. An

272 additional reference indicates that the definition has been further clarified. For some terms it
273 was not possible to clearly identify a first use.

274 Remark: Kräusel (1917) first used “araucarioid” to describe both a type of cross-field and a
275 type of a pitting on the radial wall of tracheids. Eckhold, who formalised Kräusel's ideas on
276 Protopinaceae in his thesis (1923), used the same suffix "-oid" for intertracheary radial wall
277 pitting. In order to avoid confusion it is clearer to reserve the use of this "-oid" suffix for the
278 elements of the cross-fields, and to use suffix “-ean” to describe the way intertracheary pits
279 are distributed on the radial wall.

280

281 Abietinean (Eckhold, 1923; Philippe, 1995) (Plate III, 1): a pit in the radial wall of a tracheid
282 with its “height/width” ratio equal to or higher than 1, distant from neighbouring pits. By
283 extension, a type of pitting on the radial walls of tracheids where more than 95 % of the pits
284 are of the abietinean type. See e.g. fossil-genus *Podocarpoxylon* Gothan in Gagel.

285

286 Abietineentüpfelung (Gothan, 1905): pitting of the cross walls of ray cells by contiguous
287 rounded pits (Plate I, 7; Plate V, 2 & 3). See e.g. fossil-genus *Protocedroxylon* Gothan. While
288 Gothan proposed the term in 1905, he gave a definition in 1906 only (second footnote on page
289 2). It reads as “the strong bumpy thickening of the medullary ray cell walls (horizontal and
290 vertical)” (our translation). As far as by extant woods the horizontal (i.e. radial) ray cell walls
291 can be strongly nodular without the transverse walls being pitted, it seemed sensible to
292 partially limit Gothan's definition (Philippe & Bamford, 2008).

293 Araucarian (Eckhold, 1923; Philippe, 1995) (Plate III, 2): a pit in the radial wall of a tracheid
294 with its “height/width” ratio comprised between 1 and 0.6, contiguous with at least one
295 neighbouring pit. By extension a type of pitting on the radial walls of tracheids where more
296 than 95 % of the pits are of the araucarian type. See e.g. *Agathoxylon* Hartig.

297

298 Araucarioid (Kräusel, 1917): a cross-field with several contiguous and alternate oculipores.
299 See e.g. *Agathoxylon* Hartig.

300

301 Bars of Sanio (Müller, 1890): also known as *trabeculae*, these are cylindrical bars crossing
302 the lumen of the tracheids from one tangential wall to another. When present it generally
303 appears in series and always at the same height. Its origin is not completely defined but is
304 probably exogenous, and thus it cannot be considered as having analytical value. They were

305 first described by Sanio (1873), and for a time confused with Sanio's rims (Larson, 2012).
306 Such are common e.g. by *Taxodioxyton* Hartig.

307

308 Brachyoxylean (new term) (Plate III, 3 & 4): also called mixed-type or intermediate-type or
309 transitional type (*Übergangstypus*, Eckhold, 1923), this is a type of pitting on the radial wall
310 of tracheids where less than 90% of the pits are araucarian or abietinean or xenoxylean. See
311 e.g. *Brachyoxylon* Hollick & Jeffrey.

312

313 Circopore (Marguerier and Woltz, 1977) (Plate V, 6 & 8): this type of cross-field oopore was
314 first described by Kräusel (1949: 156) as circular, or at most radially oval, but never obliquely
315 elliptic. Later Vogellehner (1968) defined circoporoid as a type of cross-field with "one,
316 rarely two, large round to broadly elliptic but never inclined oopores occupying the whole
317 field". See e.g. *Circoporoxylon* Kräusel (recently reviewed in Xia et al., 2020).

318

319 Cupressoid (Kräusel, 1917; Richter et al., 2004): an oculipore with an oblique pore (or
320 aperture), included within the limit of the pit border, usually broadly bordered. See e.g.
321 *Cupressinoxylon* Göppert (nom.cons., see Bamford et al., 2002).

322

323 Dacrydioid (Greguss, 1967) (Plate V, 6 & 9): a relatively small (occupying less than half the
324 whole field area) round circopore See e.g. *Dacrydioxyton* P. Greguss ex A. Selmeier.

325

326 False ring (Christison, 1891) (Plate I, 5 & 6): also known as "false latewood band", "double
327 growth ring", "intra-annual growth ring" or "intra annual density fluctuation (IADF)"; the
328 term of false-ring was used for both symmetric rings and asymmetric but laterally
329 discontinuous rings. Symmetric false rings are marked by a more or less gradual decrease in
330 the tracheid diameter and increase in the wall thickness (like in true latewood), after which
331 there is a smooth transition back to larger lumens and thinner tracheid cellular walls.

332 Glyptostroboid (Kräusel, 1917) (Plate V, 6): a cross field with numerous isodiametric small
333 rounded oopores. See e.g. *Glyptostroboxylon* Conwentz.

334

335 Idioblastic cell / Idioblast (not sensu Nägeli, 1884) (Plate V, 4 & 5): Idioblasts are cells
336 conspicuously different from surrounding cells. They are isolated and usually swollen. They
337 can contain tannins, oils, crystals or other material. They are uncommon in tracheidoxyls. See
338 e.g. *Ecpagloxylon* Philippe, Cuny & Bashforth, *Eristophyton* M.D. Zalesky.

339
340 Juniperustüpfelung (Gothan, 1905) (Plate V, 2 & 3): pitting of the cross walls of ray cells by
341 scalariform pits. See e.g. *Juniperoxylon* C.Houlbert
342
343 Manoxylic (Plate I, 2) Seward 1917- The terms "manoxylic" and "pynoxylic" were originally
344 introduced by Seward (1917) to differentiate the looser-textured and parenchymatous extant
345 cycadean wood from the more compact extant coniferous wood. Since a continuum of
346 tracheid diameter, tracheid/parenchyma cell proportion and ray frequency could be noticed in
347 numerous species, Galtier (1992) introduced quantitative features to complete Seward's
348 definition. According to Galtier (1992), manoxylic wood show 1) large diameter tracheids (up
349 to 150 μm), 2) large rays, both broad (more than 5 cells width) and tall (up to 200 cells high).
350
351 Oculipore (Torrey, 1923): an areolate cross-field half-pit (semi-areolate pit – half-bordered
352 pit), the border can be narrower than or broader than the pore ("resembles the conventional
353 figure of an eye", Torrey, 1923). See e.g. *Taxodioxyton* Hartig.
354
355 Oopore (Kraus, 1864): an unbordered (or simple) cross-field pit. Most authors admit that
356 oopores can be occasionally narrowly bordered. See e.g. *Xenoxylon* W. Gothan.
357
358 Phyllocladoid (Gothan, 1905; Kräusel, 1917) (Plate V, 6 & 7): an oblique elongated oopore,
359 usually with pointed tips. See e.g. *Phyllocladoxyton* W.Gothan.
360
361 Pinoid (Thinon1994) (Plate V, 6): a cross-field with pits of various sizes and shapes,
362 areolated or not. See e.g. *Pinuxylon* W.Gothan.
363
364 Podocarpoid (Gothan, 1905) (Plate V, 6): an oculipore with an oblique to almost vertical slit-
365 like to narrowly linear pore. See e.g. *Protopodocarpoxyton* W.Eckhold (nom.cons., see.
366 Bamford et al., 2002).
367
368 Pynoxylic (Plate I, 1) Seward 1917 – see manoxylic- Pynoxylic wood designate dense and
369 compact wood composed mainly of tracheids (instead of parenchyma) as in conifers.
370 According to Galtier (1992), pynoxylic woods show a combination of 1) small diameter of
371 tracheids (less than 50 μm), 2) small size of rays, both uniseriate and short.
372

373 Rim of Sanio (Groom and Rushton, 1913) (Plate IV, 1 & 2): Rims of Sanio (or Sanio's rim or
374 crassulae) are thickenings in the primary wall and the middle lamella. They are associated
375 with the bordered pits and are best observed on the radial wall of the axial tracheids. They
376 were first described by Sanio (1873) and often confused with Sanio's bars (Larson, 2012)
377 (figure). See e.g. some *Taxodioxyton* Hartig.

378

379 Septa (e.g. Thomson, 1913) (Plate IV, 8): The term has been used to refer to two different
380 things: occasional perpendicular partitioning of the tracheids, including primary and
381 secondary walls; and structures of unknown nature, not belonging to the normal cell wall.
382 These are not to be confused with trabeculae (figure). The first type of structure was described
383 by Thomson (1913) and is to be found e.g. in *Dadoxylon arduennense* Lemoigne & Demarcq
384 (Lemoigne and Demarcq, 1967), while the second is especially common in *Xenoxylon*
385 (Arnold, 1952; Medlyn and Tidwell, 1975; Philippe et al., 2013).

386

387 Shimakurean (new term = japonicum-type in Philippe et al., 2014) (Plate III, 5): a type of
388 pitting on the radial walls of tracheids where pits are contiguous, biseriate, opposite, square-
389 shaped. See e.g. *Shimakuroxyton* Philippe, Boura, Oh & Pons.

390

391 Taxodioid (Kräusel, 1917; Richter et al., 2004) (Plate V, 6): a narrowly bordered oculipore,
392 with a broad elliptic included pore. See e.g. *Taxodioxyton* Hartig.

393

394 Tracheidoxyl (Creber, 1972) (Plate I, 1): a detached portion of wood characteristically
395 composed of tracheids with only a minor proportion of other tissues (figure).

396

397 Xenoxylean (Philippe et al., 2013) (Plate III, 6): a type of pit in the radial wall of a tracheid
398 with its "height/width" ratio lower than 0.6. By extension, a type of pitting on the radial walls
399 of tracheids where more than 95 % of the pits are of the xenoxylean type (figure).

400 Characteristic of *Xenoxylon* W.Gothan.

401

402 5 Conclusion

403 New elements are presented in the hope of facilitating a more standardized description of
404 tracheidoxyls. Only this will allow truly effective comparisons to be made. Coupled with a
405 nomenclatural framework finally freed from the many oddities accumulated by a practice not

406 very attentive to the rules of the ICN, more formalized descriptions will allow one to use all
407 the enormous potential of fossil softwoods for paleoecology or paleogeography.
408 The next challenge remains the production of a taxonomic key that is not limited to the
409 Mesozoic like that of Philippe and Bamford (2008) but takes into account all the diversity of
410 the tissue that, at least in terms of biomass, has dominated continental ecosystems for nearly
411 300 million years.

412

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420

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608 Plate captions:

609 Plate 1. Fig. 1-6- Transverse section (Trs); 1- Tracheidoxyl (pycnoxylic wood), *Xenoxylon*
610 *phyllocladoides* Gothan, Gothan 117, Swedish Museum of Natural History; 2- Manoxylic wood,
611 *Medullosa* sp., Collection Roche (n°1166), MNHN, Paris ; 3- Type D & E of growth rings, *Cedroxylon*
612 *cedroides* Gothan, S1944, Swedish Museum of Natural History; 4- Type D & E of growth rings,
613 Indeterminate conifer, VI41, paleontological collections of the Université de Poitiers; 5- False rings,
614 *Callitrixylon gallicum* Privé et Boureau, 5190, Sorbonne Université ; 6- Double rings, indeterminate
615 conifer mentioned in Pons & Henri (1992); 7- Tangential longitudinal section (Tls),
616 abietineentupfelung and occurrence of intercellular spaces between ray cells, *Protopiceoxylon*
617 *extinctum* Gothan, S1909, Swedish Museum of Natural History Scale bars: 7 = 100 µm; 3 = 180 µm;
618 2 & 4 = 500 µm; 1 & 5 = 1 mm; 6 = 1 cm.

619

620 Plate 2. Fig. 1- Tls, heterocellular rays, *Ecplagloxyton mathiesenii* Philippe, Cuny & Bashforth,
621 Mathiesen 108, Natural History Museum of Denmark, Copenhagen; 2- Longitudinal radial section
622 (Lrs), heterocellular ray with a ray tracheid, *Protocedroxylon* sp., S136049, Swedish Museum of
623 Natural History; 3 – Tls, fusiform ray without a resin canal, *Thylloxyton irregulare* Gothan, S1663,
624 Swedish Museum of Natural History; 4- Trs, shape of the axial section of the tracheids circular,
625 *Ginkgoxyton quangnamense* Serra, 2682, Sorbonne Université ; 5- Trs, shape of the axial section of
626 the tracheids polygonal, *Xenoxylon phyllocladoides* Gothan, Gothan 117-2, Swedish Museum of
627 Natural History. Scale bars: 1, 2, 3 = 50 µm; 4, 5 = 200 µm.

628

629 Plate 3. Fig.1. Lrs, abietinean radial pitting, *Cupressinoxylon eocenicum* Dupéron-Laudoueneix, 9607,
630 Sorbonne Université; 2- araucarian radial pitting, *Agathoxyton trungphanense* (Vozenin-Serra) Boura
631 et al., 17, Sorbonne Université ; 3- brachyoxylean radial pitting, *Brachyoxylon notabile* Hollick &
632 Jeffrey, unnumbered specimen of drawer 68, Swedish Museum of Natural History; 4- brachyoxylean
633 radial pitting, *Brachyoxylon* sp., Oliver's collection 2200, British museum of natural history; 5-
634 shimakurean radial pitting; *Dadoxylon japonicum* Shimakura, Shimakura 53325 bis, Tohoku University
635 Museum; 6- Lrs, tracheid pits shape xenoxylean, *Xenoxylon meisteri* Palibin & Jarmolenko,
636 Shimakura 62068, Tohoku University Museum; 7- Lrs, tracheid pits shape scalariform, *Ecplagloxyton*
637 *mathiesenii*, Mathiesen 108, Natural History Museum of Denmark, Copenhagen; 8- Lrs, tracheid
638 pitting seriation in distinct bands, *Callixylon newberryi* (Dawson) Elkins & Wieland, *collections of the*
639 *University of Michigan Museum of Paleontology*; 9- Lrs, radial pits in clusters, *Pinoxylon yabei*
640 Shimakura, Shimakura 30556, Tohoku University Museum. Scale bars: 1, 9 = 50 µm; 2, 3, 4, 5, 6, 7, 8
641 = 100 µm.

642

643 Plate 4. Fig. 1- Tls, rims of Sanio, *Cedroxylon cedroides*, S1944, Swedish Museum of Natural History;
644 2- Tls, rims of Sanio, *Protocedroxylon* sp., S136049, Swedish Museum of Natural History; 3- Tls,
645 bordered pits present on the tangential walls of the axial tracheids, indeterminate conifer, VI38,
646 paleontological collections of the Université de Poitiers; 4- Lrs, Mineral contents in tracheids,
647 *Piceoxylon transiens* Gothan, Shimakura 58450, Tohoku University Museum; 5 -Rls, tracheid tips club
648 shaped, *Ginkgoxylon quangnamense* Serra, 2687, Sorbonne Université; 6- Tls (6) and Rls (7), tylosis in
649 tracheids, *Protophyllocladoxylon thylloides* Serra, 2698, Sorbonne Université; 8- Tls, septae,
650 *Metapodocarpoxydon libanoticum* (Edwards) Dupéron-Laudoueneix et Pons, 20497, Sorbonne
651 université; 9- Lrs, bars of Sanio, *Podocarpoxydon umzambicum* Müller-Stoll, SMB9666-16,
652 Senckenberg Museum, Frankfurt. Scale bars: 1, 2, 6, 7 = 50 µm; 2, 5, 8 = 100 µm; 3, 4 = 200 µm; 9 =
653 50 µm.

654
655 Plate 5. Fig 1- Tls, Abietineentupfelung, *Planoxylon hectorii* Stopes, V52823, British Museum of
656 Natural History; 2 & 3- Tls, Juniperustüpfelung, *Juniperus polycarpus* K. Koch; SU701, MNHN wood
657 collection; 4- Tls, idioblastic cells, *Ginkgoxylon quangnamense* Serra, UPMC 2687, Sorbonne
658 Université ; 5- Tr, - idioblastic cells, *Ecplagloxylon mathiesenii*, Mathiesen 108, Natural History
659 Museum of Denmark, Copenhagen ; 6- Cross field pits diversity; 7- Phyllocladoid oopores,
660 *Podocarpoxydon* sp., 5937, Sorbonne Université; 8- Circopores, *Circoporoxylon tibetense* Guoqing Xia
661 et al., PMOL-B-01497, Palaeontological Museum of Liaoning, China (courtesy of Tian Ning); 9-
662 Podocarpoid oculipores (in the late wood on the left side), *Xenoxylon phyllocladoides* Gothan,
663 Gothan 117, Swedish Museum of Natural History. Scale bars: 1, 4 = 100 µm; 5, 8 = 50 µm; 2, 3, 7, 9 =
664 20 µm.

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