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How deep is the conflict between molecular and fossil evidence on the age of angiosperms?

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1   *Tansley review*

2   **How deep is the conflict between molecular and fossil evidence on the age of angiosperms?**

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Summary

The timing of the origin of angiosperms is a hotly debated topic in plant evolution. Molecular dating analyses that consistently retrieve pre-Cretaceous ages for crown-group angiosperms have eroded confidence in the fossil record, which indicates a radiation and possibly also origin in the Early Cretaceous. Here we evaluate paleobotanical evidence on the age of the angiosperms, showing how fossils provide crucial data for clarifying the situation. Pollen floras document a Northern Gondwanan appearance of monosulcate angiosperms in the Valanginian and subsequent poleward spread of monosulcates and tricolpate eudicots, accelerating in the Albian. The sequence of pollen types agrees with molecular phylogenetic inferences on the course of pollen evolution, but it conflicts strongly with Triassic and early Jurassic molecular ages, and the discrepancy is difficult to explain by geographic or taphonomic biases. Critical scrutiny shows that supposed pre-Cretaceous angiosperms either represent other plant groups or lack features that might confidently assign them to the angiosperms. However, the record may allow the late Jurassic existence of ecologically restricted angiosperms, like those seen in the basal ANITA grade. Finally, we examine recently recognized biases in molecular dating and argue that a thoughtful integration of fossil and molecular evidence could help resolve these conflicts.

Key words: angiosperms, paleobotany, palynology, molecular dating, Jurassic, Cretaceous

I.   Introduction

The age of the angiosperms is a long-standing topic of debate. Beginning with Darwin, many botanists took the supposedly sudden appearance of diverse angiosperm leaves in the mid-Cretaceous as evidence that the group originated and radiated extensively before the Cretaceous in some area with no known fossil record. For example, Axelrod (1952, 1970) hypothesized that angiosperms originated in tropical uplands in the Permo-Triassic but only invaded lowland basins in the Cretaceous. In the 1960s, opinion began to shift toward the view that angiosperms

58   originated not long before their Cretaceous appearance. Scott *et al.* (1960) and Hughes (1961)

59   stressed the failure of palynologists to find angiosperm pollen in pre-Cretaceous rocks, despite

60   nearly worldwide sampling, arguing that some pollen should have been transported into lowland

61   basins even if angiosperms were restricted to the uplands. They also rejected reports of Triassic

62   and Jurassic angiosperms that earlier authors had cited as support for a pre-Cretaceous origin.

63   Others noted that the first Cretaceous angiosperm pollen was much less diverse than expected

64   from earlier leaf identifications, and pollen morphological types appeared in an order

65   corresponding to the course of pollen evolution inferred from comparative studies of extant

66   plants (Doyle, 1969; Muller, 1970). Subsequent workers reinterpreted the record of angiosperm

67   leaves (Hickey & Doyle, 1977) and flowers (Friis *et al.*, 2011) as showing a similar pattern of

68   diversification. Some authors took these observations as evidence that angiosperms originated in

69   the Cretaceous, but others cautioned that they might allow an earlier origin if pre-Cretaceous

70   angiosperms were at a low level of morphological diversification (Doyle, 1969; Muller 1970).

71

72   By contrast, in the past three decades a great number of molecular dating analyses, based on the

73   divergence of DNA sequences of living plants, have supported a pre-Cretaceous origin of crown-

74   group angiosperms (see Box 1 for definitions) – sometimes Jurassic, but sometimes Triassic or

75   even Permian (see Magallón *et al.*, 2015 and references therein). Late Jurassic ages might be

76   consistent with the existence of low-diversity and ecologically restricted angiosperms (Feild *et*

77   *al.*, 2004), but older dates are hard to reconcile with the congruence of the fossil record and

78   neobotanical ideas on the evolution of pollen, leaves, and flowers, which have been

79   independently confirmed by molecular phylogenetic analyses (Doyle, 2012). There have been

80   new reports of pre-Cretaceous angiosperm fossils, but these have been questioned on various

81   grounds (Doyle, 2012; Herendeen *et al.*, 2017).

82

83   Most molecular studies have not addressed these conflicts directly, but recently Barba-Montoya

84   *et al.* (2018) argued that they reflect deep flaws in interpretation of the fossil record. In this

85   review we summarize paleobotanical evidence on the early history of the angiosperms,

86   organizing our discussion around the particularly extensive pollen record. We show that an

87   informed reading of the fossil record may be consistent with a later Jurassic origin of crown-

88   group angiosperms, but it militates against an older origin, and proposed direct fossil evidence

89   for the existence of angiosperms in the Triassic and Jurassic is either erroneous, highly

90   questionable, or inconclusive. We then discuss potential biases in molecular dating analyses that

91   may have contributed to the conflict between fossil and molecular data and consider briefly the

92   future role of fossil data.

93

94   **II.   Patterns in the Cretaceous record**

95

96   In this survey, we concentrate on the pollen record, which is far better sampled spatially and

97   temporally than the record of other plant parts. Before the Aptian (Fig. 1), practically the only

98   convincing angiosperm megafossils are from the Barremian Las Hoyas flora of Spain (Gomez *et*

99   *al.*, 2015) and the Yixian flora of northeastern China (Sun *et al.*, 2002, 2008), which straddles the

100 Barremian-Aptian boundary (Chang *et al.*, 2017). Fossil flowers (usually mesofossils, in the

101 millimeter size range, which often have pollen in stamens or on stigmas) are easier to associate

102 with modern clades than pollen, but their record is still limited to relatively few formations,

103 mostly Albian and younger in age. By contrast, there is an extensive pre-Aptian pollen record of

104 angiosperms.

105

106 Some early workers took the first appearance of tricolpate pollen (now known back to the late

107 Barremian) as the first definite record of angiosperms (e.g., Scott *et al.*, 1960; Brenner, 1963).

108 Tricolpate pollen (Box 1) certainly represents evidence for crown-group angiosperms, since it is

109 the most securely established morphological synapomorphy of the eudicot clade, which includes

110 ca. 72% of living angiosperm species and is strongly supported as monophyletic by molecular

111 data. Tricolpate pollen was modified within eudicots into derived types such as tricolporate (the

112 most common type today) and triporate. However, many angiosperms have monosulcate pollen

113 (Box 1), which has long been considered ancestral based on its association with other "primitive"

114 features and its occurrence in gymnospermous seed plants (Wodehouse, 1936; Takhtajan, 1959).

115 Significantly, palynological work in the 1960s showed that the first fossil tricolpates are

116 preceded by monosulcate angiosperm pollen (Doyle, 1969; Muller, 1970). Subsequently, the

117 ancestral status of monosulcate pollen has been amply confirmed by molecular phylogenetics

118 (Doyle, 2005). Eudicots are one of five clades making up the Mesangiospermae, which include

119 99.9% of angiosperm species, along with monocots, Magnoliidae, Chloranthaceae, and the

120   aquatic genus *Ceratophyllum*. The remaining 0.01% constitute the basal "ANITA" lines, namely

121   *Amborella*, Nymphaeales (water lilies), and Austrobaileyales. All of these groups except eudicots

122   have monosulcate pollen or non-tricolpate pollen types thought to be derived from monosulcate

123   (e.g., disulculate, zonasulculate, inaperturate: Box 1).

124

125   The concept of tricolpates as the first definite evidence of crown angiosperms was reaffirmed by

126   Barba-Montoya *et al.* (2018), who took the well-nested position of eudicots as support for a long

127   prior history of angiosperms. They recognized the existence of an earlier monosulcate phase but

128   considered it phylogenetically ambiguous. However, this phase is actually quite extensive and

129   informative. In the following sections we survey the monosulcate and subsequent phases and

130   their phylogenetic implications. For a quantitative assessment of the congruence of the pollen

131   record with molecular dating studies, we complement this survey with an analysis of the

132   diversity of major pollen types through time predicted by a dated molecular tree.

133

134   **Temporal and spatial patterns in the pollen record.** The first indication of a monosulcate

135   phase in the angiosperm record was the description by Couper (1958) of *Clavatipollenites* from

136   the Barremian (upper Wealden) of England. This fossil differs from the monosulcate pollen of

137   gymnosperms in having columellar exine structure, with radial rods connecting the inner

138   (nexine) and outer (tectum) layers (Doyle *et al.*, 1975; Fig. 1). Later SEM studies (Hughes *et al.*,

139   1979) showed that Couper's (1958) material consisted of several types that differ in

140   microsculpture, but they are all columellar and reticulate, with the tectum consisting of bridges

141   (muri) linking the heads of the columellae to form a network. Many authors have used the name

142   *Clavatipollenites* for finely reticulate pollen with spinules on the muri and a sculptured sulcus.

143   TEM studies (Doyle *et al.*, 1975; Walker & Walker, 1984) showed that Aptian pollen of this type

144   from the Potomac Group of the eastern USA is also angiosperm-like in lacking the laminated,

145   distinctly staining inner nexine layer (endexine) all around the grain in gymnosperms. Instead,

146   endexine is restricted to the sulcus, and the rest of the nexine consists of ectexine (foot layer),

147   like the columellae and tectum.

148   Intensive SEM studies on the Wealden (Hughes *et al.*, 1979; Hughes & McDougall, 1990;

149   Hughes, 1994) showed low-frequency but diverse angiospermous monosulcates extending back

150   to the Hauterivian, which vary in coarseness of the reticulum and microsculpture of the muri. A

151 divergent element is *Tucanopollis* ("Barremian-*ring*" of Hughes, 1994), first described from the

152 Barremian and Aptian of Brazil (Regali *et al.*, 1974; Regali, 1989), which has a continuous

153 rather than a reticulate tectum but internal exine structure and sulcus sculpture like

154 *Clavatipollenites* (Doyle & Hotton, 1991).

155

156 In the 1970s, it became clear that some aspects of the pollen record in other geographic areas

157 differed from what is seen in England and the eastern USA. These differences indicate that there

158 are migrational as well as evolutionary patterns in the record, but they do not contradict the

159 general evolutionary scheme. The British and Potomac floras represent Brenner's (1976)

160 Southern Laurasia province, which extends east to Kazakhstan and China. The data support a

161 modified version of the poleward migration theory of Axelrod (1959), originally based on leaf

162 floras. The picture is summarized in Fig. 2, with four paleogeographic maps showing important

163 pollen sequences, selected because they are particularly well studied and well dated by marine

164 fossils or by palynological correlations with marine sediments in the same province, and Fig. 3,

165 with first occurrences in these sequences of monosulcate and tricolpate angiosperm pollen,

166 plotted against paleolatitude and time. These sequences are only a fraction of those that are

167 known, but most others are less intensively studied, less confidently dated, and/or cover only

168 short stratigraphic intervals. Many of the publications involved are several decades old, but the

169 picture is corroborated by more recent studies in both previously and newly investigated areas.

170 An important advance was recognition that tricolpate pollen (initially with reticulate sculpture)

171 appears consistently earlier in Brenner's (1976) Northern Gondwana province, including the late

172 Barremian and Aptian of Brazil (Brenner, 1976; Regali & Viana, 1989), Gabon (pollen Zone C-

173 VII; Doyle *et al.*, 1977), and Israel (Brenner, 1976, 1996). Some occurrences originally

174 considered Aptian are now thought to be late Barremian, based in part on association with the

175 distinctive pollen genus *Afropollis*, which appears in the dated late Barremian of several areas

176 (Doyle *et al.*, 1982; Hughes & McDougall, 1990; Doyle, 1992). Non-angiospermous dominants

177 indicate arid tropical climates in some parts of this province (*Classopollis*, ephedroid pollen) and

178 wetter conditions (more fern spores) in others (Brenner, 1976, 1996; Doyle *et al.*, 1982; Mejia-

179 Velasquez *et al.*, 2018).

180　Significantly, however, Zone C-VII and older sediments in Gabon and Congo (Zones C-V and

181　C-VI: Doyle *et al.*, 1977; Doyle, 1992) and Brazil (Regali & Viana, 1989) contain many of the

182　same monosulcate angiosperm types seen in the Wealden, including reticulate monosulcates and

183　especially abundant *Tucanopollis*. Later, in Zones C-VIII and C-IX (Aptian), angiosperms are

184　more diverse, including tricolpates with striate as well as reticulate sculpture. Consistent pollen

185　sequences have been described from Egypt (Schrank, 1983, 1992; Penny, 1991; Ibrahim, 2002;

186　Schrank & Mahmoud, 2002) and Israel (Brenner, 1996). Reticulate monosulcate pollen is known

187　from the Valanginian of Israel (Brenner, 1996) and Italy (Trevisan, 1988), which was located at

188　the northern edge of Gondwana.

189　In Asian paleoequatorial areas, pre-Albian floras are like those of Northern Gondwana in their

190　non-angiospermous dominants (Smiley, 1970; Li & Liu, 1994; Racey & Goodall, 2009). In

191　South China, *Clavatipollenites* and tricolpates have been reported from presumed pre-Albian

192　beds, plus tricolpates and tricolporates from the Albian-early Cenomanian (Li & Liu, 1994), but

193　age control is poor.

194　The dynamics of relations between Southern Laurasia and Northern Gondwana are becoming

195　increasingly clear. In England, Kemp (1968) reported the first tricolpates (with reticulate

196　sculpture) in the marine early Albian, together with the distinctive *Clavatipollenites rotundus*

197　group. Similarly, in well-dated Barremian through middle Albian marine sequences in Portugal,

198　Heimhofer *et al.* (2007) found the first reticulate tricolpates and *C. rotundus* in the earliest

199　Albian, joined later in the early Albian by striate tricolpates. Reticulate and striate tricolpates

200　also occur in the late early Albian of Texas (Tanrikulu *et al.*, 2017). In the Potomac Group,

201　reticulate tricolpates and *C. rotundus* appear consistently in upper Zone I (Doyle & Robbins,

202　1977; Hickey & Doyle, 1977). However, Hughes & McDougall (1990) illustrated exceedingly

203　rare earlier tricolpates (one grain in the late Barremian, one in the early Aptian), and Doyle

204　(1992) reported two tricolpate grains in lower Zone I (presumably Aptian).

205　Although these data imply that very rare eudicots existed in Southern Laurasia since the late

206　Barremian, the consistent early Albian appearance of reticulate and striate tricolpates, which

207　occurred in Northern Gondwana since the late Barremian and early Aptian, respectively, appears

208　to represent a major migrational influx of eudicots, possibly due to global warming (Heimhofer

209   *et al.*, 2005; Coiffard & Gomez, 2012; Zhang *et al.*, 2018). The Potomac leaf record shows a

210   consistent pattern. Zone I contains rare simple angiosperm leaves comparable to members of the

211   ANITA grade, Chloranthaceae, magnoliids, and monocots, plus ternately lobed leaves. The latter

212   have been compared with the basal eudicot order Ranunculales (see Jud, 2015), but the low

213   number of vein orders, presence of mesophyll secretory cells, and absence of tricolpate pollen at

214   some localities have led to suspicions that some of these leaves may not be crown-group eudicots

215   (Doyle, 2012; Doyle & Upchurch, 2014). By contrast, Zone II (middle and late Albian) shows a

216   variety of new eudicot leaf types, as discussed below.

217   The record in Northern Laurasia (Siberia, Alaska, Canada) and Southern Gondwana (southern

218   South America, southern Africa, India, Australia, Antarctica) completes this picture by showing

219   a still more delayed entry of angiosperms. In western Canada, tricolpates are first reported in the

220   middle or late Albian (Norris, 1967; Playford, 1971; Singh, 1975). Angiospermous monosulcates

221   appear at the same horizons or slightly earlier (early middle Albian: Playford, 1971). In Arctic

222   Canada and Alaska, Brenner (1976) found no tricolpates until the Cenomanian, but they have

223   been extended down into the late Albian in the Canadian Arctic Archipelago; angiospermous

224   monosulcates are usually absent (Galloway *et al.*, 2012). In Australia, *Clavatipollenites* appears

225   in the (Barremian?) Aptian, reticulate tricolpates in the middle or late Albian (Dettmann, 1973,

226   1986; Burger, 1993; Korasidis *et al.*, 2016). In southern Argentina, *Clavatipollenites* and other

227   angiosperm monosulcates occur in the Aptian and are joined by tricolpates in the early Albian

228   (Archangelsky *et al.*, 2009; Llorens & Perez Loinaze, 2016; Perez Loinaze *et al.*, 2016). In the

229   Antarctic peninsula, *Clavatipollenites* appears in the early Albian and tricolpates in the middle

230   Albian-Cenomanian (Dettmann & Thomson, 1987).

231   These variations do not contradict the congruence of the sequence of fossil pollen types and

232   ideas on evolution based on extant plants; they simply mean that certain lines immigrated later

233   into some areas. The earlier absences of angiosperms are not a function of absence of suitable

234   rocks, since there are older sediments in many of these areas with rich pollen and spore floras but

235   no reported angiosperms (e.g., white circles in Fig. 2).

236

237   **Phylogenetic implications of pre-Aptian fossils.** A phylogenetic perspective helps to clarify

238   what Cretaceous fossils do and do not say about the early history of angiosperms. Because a

239   single sulcus is presumably ancestral in angiosperms, being shared with other seed plants and

240   inferred to extend down to the crown node on molecular trees (Fig. 1), other characters are

241   needed to infer whether monosulcate pollen represents crown-group angiosperms rather than

242   stem relatives or unrelated gymnospermous groups. Columellar exine structure is evidence for a

243   relationship to angiosperms rather than other taxa, but it does not distinguish between crown

244   group members and stem relatives.

245

246   A character that may place fossils above the crown node is a reticulate tectum, seen from the

247   Valanginian onward. This is because the first two angiosperm lines to diverge in most molecular

248   trees, *Amborella* and Nymphaeales, have columellae (reduced to short connections between the

249   tectum and the nexine in *Amborella*, crushed during development in some Nymphaeales: Doyle,

250   2005) but a continuous or microperforate tectum, whereas the third line, Austrobaileyales, has a

251   reticulate tectum, which is also basic in mesangiosperms. In terms of parsimony (Doyle, 2005;

252   Fig. 1), this implies that a reticulate tectum is a synapomorphy of Austrobaileyales and

253   mesangiosperms, and that Valanginian reticulate-columellar monosulcates are nested in the

254   crown group. However, some molecular analyses group *Amborella* and Nymphaeales as a clade

255   (e.g., Barkman *et al.*, 2000; Xi *et al.*, 2014), in which case the ancestral tectum could be either

256   continuous or reticulate. Furthermore, it is possible that in this case parsimony reconstruction is

257   confounded by long-branch effects (where the length of a branch is the product of its duration in

258   time and the rate of evolution), which might be corrected by model-based approaches (cf. Coiro

259   *et al.*, 2018). In terms of time, *Amborella* is at the end of a very long branch, on which the tectum

260   character might have more likely changed than on shorter branches, unless its rate of evolution

261   was very low. Finally, monosulcate pollen adhering to the early Albian nymphaealean flower

262   *Monetianthus* (Friis *et al.*, 2009b) is reticulate. However, because no stamens are preserved, it is

263   uncertain that this pollen is from the same species.

264

265   Despite these uncertainties, there is reason to think that many (if not all) Cretaceous reticulate

266   monosulcates and related pollen types belong to the crown group. One type that shares especially

267   distinctive synapomorphies with a modern clade consists of tetrads of monoporate pollen called

268   *Walkeripollis*, from the late Barremian of Gabon (Doyle *et al.*, 1990). Phylogenetic analysis links

269 *Walkeripollis* with Winteraceae (Doyle & Endress, 2010), which are nested within Magnoliidae,

270 the third-largest of the five mesangiosperm clades.

271

272 Other Hauterivian-Barremian pollen types resemble pollen found in stamens or on stigmas of

273 younger mesofossils that are confidently linked with extant clades. For example, pollen of the

274 *Clavatipollenites* type, with supratectal spinules and a sculptured sulcus, is associated with early

275 Albian flowers that are nested in Chloranthaceae (*Canrightiopsis*: Friis *et al.*, 2015; Doyle &

276 Endress, 2018). Similar pollen without spinules was produced by *Canrightia*, apparently a stem

277 relative of Chloranthaceae (Friis & Pedersen, 2011; Doyle & Endress, 2014, 2018). *Similipollis*,

278 with finer sculpture at the proximal pole and the sulcus margins, is associated with Albian

279 mesofossils (*Anacostia*: Friis *et al.*, 1997) that phylogenetic analyses nest within

280 Austrobaileyales (Doyle & Endress, 2014).

281

282 An intriguing case is the continuous-tectate genus *Tucanopollis*, from the Barremian-Aptian of

283 Brazil (Regali, 1989) and Gabon/Congo (Doyle *et al.*, 1977; Doyle & Hotton, 1991) and the

284 Hauterivian-Barremian of England (Hughes, 1994). It is similar to pollen of the Cenomanian

285 genus *Pseudoasterophyllites*, a presumed halophyte with reduced leaves, which has been linked

286 with *Ceratophyllum* and Chloranthaceae on molecular trees in which these taxa form a clade

287 (Kvaček *et al.*, 2016). The floating aquatic *Montsechia*, from the Barremian of Spain, has also

288 been associated with *Ceratophyllum* (Gomez *et al.*, 2015), but its pollen is unknown.

289

290 Despite being dominated by rather nondescript reticulate monosulcate pollen, the pre-Aptian

291 fossil record clearly indicates significant diversification of crown-group angiosperms, some 10-

292 15 Ma of which is represented in the pollen record. The most dramatic macromorphological

293 divergence may be the extreme vegetative and floral reduction in *Montsechia* (Gomez *et al.*,

294 2015), but we see no way to estimate how much time this required, especially if reduction in

295 aquatic lines can be unusually rapid (Cook, 1999).

296

297 These observations do not necessarily mean that all pre-Aptian angiosperm-like fossils belong to

298 the crown group; some could be persisting stem relatives. The aquatic plant *Archaefructus* from

299 the Barremian-Aptian Yixian Formation of China, with ternately dissected leaves and fertile

300   structures of controversial morphology, was proposed as such by Sun *et al.* (2002). Later

301   analyses linked it with Nymphaeales or eudicots (Doyle, 2008; Endress & Doyle, 2009), but its

302   position remains highly uncertain (Friis *et al.*, 2011; Doyle & Endress, 2014). Another candidate

303   is *Afropollis* (late Barremian to Cenomanian; Doyle *et al.*, 1982, 1990), which has a reticulate

304   tectum but a gymnosperm-like laminated endexine, and which Friis *et al.* (1999, 2011) reported

305   in microsporangia that lack angiosperm features.

306

307   **Implications of the post-Barremian record.** So far, there is no clear Barremian evidence for

308   monocots, the second-largest of the five mesangiosperm clades. However, there are monocot

309   fossils in the Aptian, including monosulcate pollen with a distinctive graded sculpture pattern

310   (*Liliacidites*) and leaves with apically fusing venation (*Acaciaephyllum*) from lower Zone I of

311   the Potomac Group (Doyle *et al.*, 2008), and vegetative remains representing the near-basal

312   monocot family Araceae from the late Aptian Crato Formation of Brazil (Coiffard *et al.*, 2013).

313

314   Several other basically monosulcate clades are known from flowers and associated leaves and

315   stems from the Aptian, Albian, and early Cenomanian. Nymphaeales are represented by

316   *Pluricarpellatia* from the Crato Formation (Mohr *et al.*, 2008) and *Monetianthus* (Friis *et al.*,

317   2009b) from Portugal (early Albian: Heimhofer *et al.*, 2007; Doyle & Endress, 2014; Tanrikulu

318   *et al.*, 2017). Among Magnoliidae, *Endressinia* and *Schenkeriphyllum* (Crato) are nested in

319   Magnoliales (Doyle & Endress, 2010; Mohr *et al.*, 2013), while *Archaeanthus* (late Albian-early

320   Cenomanian; Dilcher & Crane, 1984) is near or in Magnoliaceae (Doyle & Endress, 2010).

321   Laurales include *Virginianthus* (middle Albian; Friis *et al.*, 1994) near the base of the order and

322   *Mauldinia* (early Cenomanian; Drinnan *et al.*, 1990) linked with the derived families Lauraceae

323   and Hernandiaceae (Doyle & Endress, 2010). Piperales are represented by *Hexagyne* (Crato;

324   Coiffard *et al.*, 2014).

325

326   Like the appearance of monosulcate before tricolpate angiosperm pollen, the stratigraphic

327   succession of tricolpate and derived pollen types is consistent with evolutionary transformation

328   series proposed by earlier botanists (e.g., Takhtajan, 1959) and confirmed by molecular analyses

329   (Doyle, 2005). A series of "basal eudicot" lines with basically tricolpate pollen diverge below the

330   huge Pentapetalae or "core eudicot" clade, which is united by pentamerous flowers with

331   differentiated sepals and petals. Pentapetalae consist of two large clades, Rosidae and Asteridae,

332   and several smaller clades. Tricolporate pollen is apparently ancestral in rosids and asterids, but

333   it also originated independently in some basal eudicots (Sabiaceae, Buxaceae, Menispermaceae),

334   while both tricolpate and tricolporate pollen occurs in basal Pentapetalae such as Saxifragales,

335   Dilleniaceae, and Caryophyllales (Furness *et al.*, 2007).

336

337   The derived status of the tricolporate condition is consistent with the fact that the oldest known

338   tricolporate pollen is much younger than the first tricolpates. Tricolpate pollen with weakening at

339   the middle of the colpi (tricolporoidate) first occurs in the middle Albian and becomes common

340   in the late Albian, while types with more distinct ora appear in the latest Albian and

341   Cenomanian. Many tricolporates show shifts from reticulate sculpture to a smooth tectum and

342   triangular shape (Doyle, 1969; Pacltová, 1971; Herngreen, 1973; Laing, 1975; Singh, 1975;

343   Doyle & Robbins, 1977; Burger, 1993; Horikx *et al.*, 2016; Perez Loinaze *et al.*, 2016).

344

345   Potomac Zone II and middle and late Albian beds in Kansas (Huang & Dilcher, 1994), Spain

346   (Sender *et al.*, 2016), and Kazakhstan (Vakhrameev, 1952) contain abundant leaves and flowers

347   related to basal eudicot lines (see Doyle & Endress, 2010). These include peltate leaves

348   (*Nelumbites*) and floral receptacles related to *Nelumbo* (Upchurch *et al.*, 1994) and pinnately to

349   palmately lobed leaves (*Sapindopsis*, platanoids) and heads of unisexual flowers related to

350   *Platanus* (Friis *et al.*, 1988, 2011; Crane *et al.*, 1993), both in Proteales. Flowers with striate

351   tricolpate pollen (*Spanomera*: Drinnan *et al.*, 1991) represent stem relatives of Buxaceae.

352   *Kajanthus*, from the early Albian of Portugal (Mendes *et al.*, 2014), has been linked with

353   Lardizabalaceae in the order Ranunculales, which is sister to all other eudicots.

354

355   The oldest clear megafossil record of Pentapetalae is *Dakotanthus*, a pentamerous flower with

356   differentiated calyx and corolla, two cycles of five stamens, and tricolporate pollen from the

357   latest Albian of Nebraska (Manchester *et al.*, 2018). This is followed by *Caliciflora* in the early

358   Cenomanian of Maryland (Friis *et al.*, 2016). Flowers representing several clades of rosids and

359   asterids are known from the younger upper Raritan Formation of New Jersey (Crepet, 2008).

360

361   The next conspicuous event in the pollen record is the appearance of triangular triporate pollen

362   of the Normapolles group in the middle Cenomanian (Pacltová, 1971). Such pollen proliferates

363   later in the Cretaceous of Europe and eastern North America (Góczán *et al.*, 1967; Batten, 1981).

364   The pores have a compound structure, consistent with derivation from triangular tricolporate

365   pollen by shortening of the colpi (Doyle, 1969). Early comparisons with triporate pollen in the

366   rosid order Fagales are confirmed by association of Normapolles with fagalean flowers (Friis,

367   1983; Friis *et al.*, 2006). Triangular triporate pollen (*Triorites africaensis*) also appears in the

368   Cenomanian of Northern Gondwana (Jardiné & Magloire, 1965; Herngreen, 1973), but it appears

369   to be related to Proteaceae in the basal eudicot order Proteales (Ward & Doyle, 1994). The pores

370   are simple, consistent with origin from tricolpate pollen, as expected from the position of

371   Proteaceae.

372

373   **General evolutionary implications.** Perhaps more than the record of angiospermous

374   monosulcates, the stratigraphic record of tricolpate and derived pollen types argues against the

375   long period of unrecorded diversification implied by molecular dating analyses. This is

376   illustrated graphically by Fig. 4, based on a dated molecular tree derived from the data set of

377   Magallón *et al.* (2015), which is representative of trees with a Triassic age of angiosperms. In

378   this analysis we estimated the number of lineages with sulcate, colpate (mostly tricolpate),

379   colporate, porate, and inaperturate pollen from states in living taxa using stochastic character

380   mapping (see Methods S1 and Table S1), juxtaposed with observed curves of pollen types in

381   three Cretaceous sections. Estimated ages center on 220 Ma for angiosperms (Late Triassic), 150

382   Ma for eudicots (Late Jurassic), and 132 Ma for Pentapetalae (Hauterivian), comparable to dates

383   of Barba-Montoya *et al.* (2018). The tree implies that colpates were already nearly as diverse as

384   sulcates when they are first observed as fossils in the late Barremian, and more remarkably that

385   colporates were as diverse as colpates, ca. 20 Ma before the first tricolporate pollen is seen in the

386   late Albian. It is difficult to attribute this mismatch to failure of palynologists to recognize earlier

387   tricolpate and tricolporate pollen. It is possible to overlook monosulcate angiosperm pollen,

388   which may require close examination to distinguish from gymnospermous pollen, but tricolpates

389   and tricolporates are easily recognized, and palynologists have been aware of their relation to

390   angiosperms since early in the history of the field.

391

392   These considerations show paradoxical congruence relations among molecular phylogenetic

393   analyses, molecular dating, and the fossil record. The stratigraphic succession of pollen types is

394   congruent with scenarios for character evolution inferred from molecular phylogenetics, but not

395   with molecular dating analyses. Congruence between inferred pollen evolution and stratigraphy

396   is expected only if there was a relatively short lag between evolution of successively more

397   derived types and their appearance in the fossil record. If molecular dates of the sort in Fig. 4 are

398   correct, one must ask why taxa with new pollen types waited patiently for tens of millions of

399   years before entering the fossil record in the order they had evolved.

400

401   A related question is why angiosperms did not radiate in the Jurassic if they originated then,

402   given that they expanded so dramatically in the Cretaceous. The answer cannot be that the whole

403   suite of angiosperm innovations had not yet accumulated, because in that case Jurassic

404   representatives of the angiosperm line would be on the stem lineage rather than in the crown

405   group, and the conflict with molecular dates would remain. It is difficult to imagine extrinsic

406   environmental factors that might have suppressed radiation of angiosperms as a whole,

407   considering how quickly they occupied a wide range of climatic belts and local habitats in the

408   Cretaceous (Doyle & Donoghue, 1993). However, as argued by Feild *et al.* (2004), if Late

409   Jurassic angiosperms were like extant terrestrial members of the ANITA grade (*Amborella*,

410   Austrobaileyales), which grow mainly in wet tropical to subtropical forest understory habitats,

411   they might have been restricted geographically and inhibited from diversifying because most of

412   the tropical belt was arid at that time. The observed Cretaceous rise of angiosperms might then

413   represent the radiation of mesangiosperms. There are some Early Cretaceous fossils from the

414   ANITA grade, such as *Anacostia*/*Similipollis* in Austrobaileyales (Friis *et al.*, 1997; Doyle &

415   Endress, 2014) and a growing number of Nymphaeales. However, *Similipollis* is a minor element

416   in palynofloras, and it is possible that the nymphaealean line was still terrestrial in the Jurassic

417   and did not become widespread until it later invaded aquatic habitats (Doyle & Endress, 2014).

418

419   **Potential taphonomic biases.** Barba-Montoya *et al.* (2018) suggested that the mismatch

420   between fossil and molecular dates "may be more perceived than real" because the "orderly and

421   incrementally phased environmental invasion… may be an artefact imposed by the non-

422   uniformity of the rock record." However, this argument refers to models for the ecological

423   radiation of angiosperms proposed by Hickey & Doyle (1977) and Coiffard *et al.* (2012), based

424   on sedimentary facies associations and functional morphology of fossil leaves, not the patterns

425   stressed here. There is indeed a danger that taphonomic biases may affect some inferences, such

426   as the argument that the predominance of aquatic angiosperms in the Barremian supports an

427   aquatic origin (Coiffard *et al.*, 2012; see Box 2). It is possible that aquatic angiosperms are

428   overrepresented in the Barremian and Aptian record because of intense attention to the justly

429   famous lacustrine deposits at Las Hoyas, the Yixian Formation, and the Crato Formation, while

430   other facies with less well-preserved remains are unstudied.

431

432   By contrast, because palynological studies sample a variety of fluvial, deltaic, and nearshore

433   marine facies, and because pollen is readily transported by wind and water, the pollen record

434   should give a more comprehensive qualitative view of the angiosperm flora at a given time, as

435   argued by Muller (1970). Judging from studies on the Potomac Group (Doyle, 1969; Doyle &

436   Robbins, 1977; Hickey & Doyle, 1977), which was deposited mainly in a meandering fluvial

437   system, certain angiosperm pollen types are much more common in some samples than in others,

438   presumably because of local abundance of the source plants in particular floodplain habitats.

439   However, there is a relatively uniform lower-frequency "background" assemblage of

440   angiosperms common to most samples, which presumably includes pollen transported from

441   many habitats. Angiosperm leaves show much more facies restriction, a fact exploited by Hickey

442   & Doyle (1977) in reconstructing ecological preferences. All pollen in the intensively studied

443   nearshore marine sequence in Portugal (Heimhofer *et al.*, 2007; Horikx *et al.*, 2016) is

444   transported, doubtless from a broad spectrum of inland environments.

445

446   **III.   Pre-Cretaceous angiosperm reports**

447

448   There is a long history of reports of pre-Cretaceous angiosperms and their rejection for

449   stratigraphic or morphological reasons (Axelrod, 1952, 1970; Scott *et al.*, 1960; Hughes, 1961a;

450   Doyle, 2012; Herendeen *et al.*, 2017; Wang, 2018). Recently, molecular dating studies have cited

451   putative pre-Cretaceous angiosperms as support for early molecular ages for crown-group

452   angiosperms (e.g., Barba-Montoya *et al.*, 2018), and paleobotanists have taken molecular dates

453   as enhancing the plausibility of pre-Cretaceous claims (e.g., Liu & Wang, 2017; Wang, 2018). It

454   should be recalled that fossils relate to molecular ages of the angiosperms only if they belong to

455   the crown group; stem relatives can be either older or younger than the crown node.

456

457   Barba-Montoya *et al.* (2018) suggested that paleobotanical arguments against pre-Cretaceous

458   angiosperms are flawed because of reliance on absence of evidence for "key characters," rather

459   than evidence of their absence; formulation of key characters in "the increasingly outmoded

460   parsimony-based phylogenetic framework"; and methodological biases in distinguishing stem-

461   and crown-angiosperms. However, these issues are irrelevant in most cases. Bayesian inference

462   performs better than parsimony in cases of long-branch attraction, but it would be unwarranted to

463   dismiss results based on parsimony out of hand: both methods usually give congruent results

464   with empirical data sets (Rindal & Brower, 2011; Coiro *et al.*, 2018). No putative pre-Cretaceous

465   angiosperms have been examined in an explicit phylogenetic framework of any sort (although

466   parsimony was used to evaluate the putative Cretaceous stem fossil *Archaefructus*: Sun *et al.*,

467   2002; Doyle, 2008), and there are few cases where the issue is whether fossils are stem relatives

468   or crown-group members. Usually disagreement concerns whether morphological features were

469   misinterpreted, or whether the fossils are related to other seed plant groups. Some have defined

470   angiosperms typologically (plants with enclosed seeds) while neglecting evidence for the

471   homology of the structures involved or characters of other organs. There are similar problems

472   with some Cretaceous fossils (see Herendeen *et al.*, 2017), but here we focus on pre-Cretaceous

473   records (for more details of our interpretations of particular taxa, see Notes S1).

474

475   Several fossils cited by Axelrod (1952) and others as pre-Cretaceous angiosperms were later

476   shown to belong to other plant groups that were unrecognized at the time. A classic example is

477   *Eucommiidites*, a Jurassic and Cretaceous pollen type with three furrows that Erdtman (1948)

478   compared with the tricolpate pollen of eudicots. Confirming earlier less conclusive indications

479   (e.g., Couper, 1958; Doyle *et al.*, 1975), Pedersen *et al.* (1989) and Friis *et al.* (2009a) associated

480   *Eucommiidites* with male and female structures that they assigned to the new order

481   Erdtmanithecales, which is apparently related to Gnetales.

482

483   A recent example of this sort is *Schmeissneria*, described from the Early Jurassic of Germany by

484   Kirchner & van Konijnenburg-van Cittert (1994) as a ginkgophyte. It has short shoots bearing

strap-shaped leaves with an even number of veins; attached female axes bearing units consisting of one or two seeds surrounded by a longitudinally ridged "cupule"; and male axes bearing sporophylls with a cluster of pollen sacs, which are not known attached but occur consistently in the same beds. Wang *et al.* (2007) and Wang (2010, 2018) reinterpreted the female units in the German fossils and Middle Jurassic material from China as flowers with a perianth and two fused carpels with enclosed ovules. Wang *et al.* (2007) rejected the ginkgophyte interpretation because Kirchner & van Konijnenburg-van Cittert (1994) had excluded *Schmeissneria* from all known ginkgophyte genera; however, this only meant it was a new genus and in no way excluded it from ginkgophytes as a whole, which it resembles in all the vegetative and male features listed. To this list van Konijnenburg-van Cittert (2010) added smooth monosulcate pollen, which is typical of (though not limited to) ginkgophytes. Furthermore, the female units can be reinterpreted in ginkgophytic terms, with the carpels as seeds (with apical hairs, as argued by Wang, 2010), and the supposed enclosed seeds, which show no regular relation to the ridges of the cupule and no cellular detail, as resin bodies in the cupule wall. The cupule may correspond to the bivalved capsule of the ginkgophytic order Czekanowskiales, which differs in containing several seeds rather than one or two. Wang *et al.* (2007) and Wang (2010) described the female structures as having two locules separated by a septum, but identification of such internal features often requires three-dimensional preservation, whereas these fossils are nearly two-dimensional compressions. The reconstruction of *Schmeissneria* presented by Wang (2018) is most un-angiosperm like, but it closely conforms to the morphology of a ginkgophyte group such as Czekanowskiales.

A similar case is *Solaranthus*, from the Middle Jurassic of China, which Zheng & Wang (2010) interpreted as a flower with numerous carpels on a peltate receptacle and reflexed tepals and stamens. Deng *et al.* (2014) synonymized *Solaranthus* with *Aegianthus* (a resemblance already noted by Zheng & Wang, 2010), which has peltate microsporophylls with pollen sacs below the polygonal cap and resin bodies in the cap. They considered *Aegianthus* a cycad, but because its microsporophylls are nearly radial, while those of cycads are bilateral, a more likely relationship may be with the "seed fern" order Peltaspermales. The smooth monosulcate pollen would be consistent with either affinity. The supposed carpels appear to be resin bodies in the cap, while the stamens and tepals are clearly pollen sacs viewed at various angles. Their reflexed orientation

516 would be typical for cycad or peltasperm pollen sacs but bizarre for parts of a flower. Wang

517 (2018) discounted the interpretation of Deng *et al.* (2014) but offered no additional evidence for

518 *Solaranthus* being anything other than a gymnosperm pollen organ.

519

520 Liu & Wang (2016) described *Euanthus* from the Middle Jurassic of China as a flower with

521 sepals, petals, anthers, and a gynoecium with an apical style and pentamerous ovary. However,

522 the texture of the supposed sepals and petals is distinctly woody, more like the cone scales of a

523 conifer than perianth parts of an angiosperm, as illustrated graphically by Herendeen *et al.*

524 (2017). The style may represent the cone axis where scales have fallen off, but it is not clear

525 whether it is actually part of the specimen or just underlies it. The pentamerous receptacle

526 appears to be a basal view of the broken cone axis and surrounding smaller scales, while the so-

527 called anthers (Liu & Wang, 2016; Wang, 2018) have no clear morphological features. Overall,

528 *Euanthus* is more readily interpreted as a fragmentary conifer cone than an angiosperm flower.

529

530 A similar case may be *Nanjinganthus* from the Early Jurassic of China (Fu *et al.*, 2018), known

531 as numerous compressions with a "perianth" of appendages similar to those of *Euanthus*, with

532 ridges suggesting robust vascular bundles. Ten specimens have a branched prolongation of the

533 axis described as a "dendroid style." This resembles an axis with spirally arranged appendages

534 more than the style of any angiosperm. It recalls the male cones of some conifers, which have

535 basal bracts resembling the "perianth." Fu *et al.* (2018) rejected this interpretation because they

536 found no pollen on the dendroid structure, but this could be due to loss at many points prior to

537 burial. Alternatively, the "style branches" may be degraded ovuliferous scales of a female

538 conifer cone. Fu *et al.* (2018) interpreted the basal part of the fossils as an inferior ovary with 1-3

539 enclosed ovules, but the morphology of this area is obscure because of poor preservation and

540 irregularity in the number and appearance of the supposed ovules.

541

542 Other proposed pre-Cretaceous angiosperms are less clearly related to any particular non-

543 angiospermous group but show little evidence of homologies with angiosperm structures, or have

544 anomalous features that cast doubt on such homologies. One is *Xingxueanthus*, from the Middle

545 Jurassic of China (Wang & Wang, 2010; Wang, 2018), interpreted as an axis with bracts and

546 axillary gynoecia with free-central placentation. However, the supposed axis of the flower

547   (placenta) is perpendicular to the bract and parallel to the axis, not at an angle arising from the

548   axil. The presence of a bract subtending the "gynoecium" and the woody appearance of the

549   "placenta" could indicate that this fossil represents the ovuliferous shoot of a coniferophyte, but

550   again it is highly compressed, and the morphological nature of its parts is obscure.

551

552   Two other fossils from the Middle Jurassic of China have herbaceous leafy stems. Han *et al.*

553   (2016) described *Juraherba* as consisting of a corm-like stem bearing roots, linear one-veined

554   leaves, and axes terminating in longitudinally ridged fructifications that contain seeds. One-

555   veined leaves occur in a few angiosperms, such as Hydatellaceae in the Nymphaeales (as noted

556   by Han *et al.*, 2016), but they are more typical of lycophytes and conifers. The ridges appear to

557   be narrow pointed appendages of a strobilus; the supposed seed lacks any visible structure.

558   *Yuhania* (Liu & Wang, 2017) consists of a stem bearing linear leaves with 5-6 parallel veins and

559   structures described as aggregate fruits. However, the putative fruits vary in size by an order of

560   magnitude, and the one with the most visible structure (fig. 2h) is not clearly attached. Liu &

561   Wang (2017) and Wang (2018) interpreted the units making up the fruits as carpels subtended by

562   bracts (contrary to the definition of an aggregate fruit as derived from one flower with free

563   carpels), but the supposed bracts and carpels have a highly anomalous reflexed orientation, and

564   the structures identified as seeds have no visible morphology. Better preserved specimens of

565   these enigmatic plants are required to obtain enough detail for robust systematic conclusions.

566

567   A somewhat similar case is *Sanmiguelia*, originally based on pleated leaves from the Late

568   Triassic of Colorado (Brown, 1956). Cornet (1986, 1989) associated Late Triassic leaves from

569   Texas with woody stems and male and female structures, the latter as interpreted as flowers with

570   a perianth and several carpels. He argued that the leaves are monocot-like in having two orders

571   of parallel venation and cross-veins, but the low frequency and irregularity of the cross-veins

572   suggest they may be artifacts of degradation and shredding of leaf tissue. The male organs are

573   strobili that appear more ginkgophytic than angiospermous; the pollen is smooth and

574   monosulcate, consistent with many possible affinities. The female organs are so highly

575   compressed that features such as enclosed seeds are not demonstrable (Doyle & Donoghue,

576   1993). The leaf morphology might be most plausibly derived from a coniferophyte (ginkgophyte,

577   conifer, gnetophyte) type with an even number of parallel veins.

578

579 A general problem is that the proposed Jurassic angiosperms known as isolated reproductive

580 structures (*Solaranthus*, *Euanthus*, *Nanjinganthus*, *Xingxueanthus*) occur in compression floras

581 that are rich in typical Jurassic ferns, ginkgophytes, cycadophytes, and conifers (e.g., Na *et al.*,

582 2017; Pott & Jiang, 2017; Fu *et al.*, 2018) but contain no leaves with distinctive angiosperm

583 apomorphies (several orders of reticulate venation, etc.), while those known as nearly whole

584 plants (*Schmeissneria*, *Juraherba*, *Yuhania*) have leaves with no angiosperm features. By

585 contrast, in Cretaceous and Cenozoic impression and compression floras, flowers are far less

586 common than leaves of the same taxa. If the Jurassic fossils were angiosperm stem relatives they

587 might not have typical angiosperm leaves, but they would also have no bearing on molecular

588 ages. Furthermore, one would expect angiosperms to be more like each other in the Jurassic than

589 in the Early Cretaceous, but if anything proposed Jurassic angiosperms are more disparate

590 morphologically and lack common features that might provide a coherent picture of the first

591 angiosperms.

592

593 There are pre-Cretaceous fossils that share clearer potential synapomorphies with angiosperms.

594 These include the Late Triassic Crinopolles pollen group, first described by Cornet (1989) from

595 the Newark sequence of Virginia, which includes monosulcate pollen with columellae and a

596 reticulate tectum. However, in well-preserved specimens, TEM shows that the nexine consists of

597 laminated endexine of uniform thickness (Cornet, 1989; Doyle & Hotton, 1991; Fig. 5a-d), as in

598 gymnospermous pollen, whereas in Early Cretaceous and extant monosulcate angiosperms

599 endexine is either lacking or non-laminated, except under the sulcus (Doyle *et al.*, 1975). This

600 could mean that Crinopolles represent either a convergent gymnospermous group or angiosperm

601 stem relatives. As discussed above, it is not resolved whether the ancestral tectum in

602 angiosperms was continuous or reticulate. Reticulate-columellar monosulcates are also known

603 from the Middle Triassic of the Barents Sea and Switzerland (Hochuli & Feist-Burkhardt, 2004,

604 2013), but their nexine structure is unknown.

605

606 Equally tantalizing is *Phyllites* sp. of Seward (1904) from the Middle Jurassic Stonesfield Slate

607 of England (see also Cleal & Rees, 2003; Fig. 5e,f). This is a single ovate leaf with acrodromous

608 venation (palmate venation with a midvein and arcuate lateral primary veins). Unfortunately no

609   cuticle or finer venation is preserved, so it is not known if there were several orders of reticulate

610   veins. The major venation suggests a position in the crown group, since in terms of parsimony

611   ovate leaf shape is ancestral but palmate venation is derived, arising in Nymphaeales, Piperales,

612   some Laurales, and eudicots (Doyle, 2012).

613

614   **IV.   Potential biases in molecular dating**

615

616   This survey indicates that the angiosperm fossil record is indeed difficult to reconcile with

617   molecular analyses that date the angiosperm crown group as much older than the Cretaceous, and

618   the conflict cannot be readily explained as a result of misinterpretation of the fossil record.

619   Molecular dating analyses have sometimes been perceived as more trustworthy, because they

620   supposedly overcome biases and weaknesses of the fossil record (e.g., Kenrick, 2011). However,

621   molecular dating methods are not free from their own potential sources of bias, and not

622   necessarily as accurate as desired, or as robust against violation of their many assumptions

623   (Bromham *et al.*, 2018).

624

625   Cases in which molecular analyses estimate a much older age than fossil evidence in other

626   groups, such as mammals (dos Reis *et al.*, 2012; O'Leary *et al.*, 2013; Phillips & Fruciano,

627   2018), have led others to reinvestigate the assumptions of molecular dating. Indeed, even though

628   new methods to deal with issues such as rate heterogeneity and topological error are constantly

629   being developed, it could be that some biological problems are still outside the scope of our

630   current implementations.

631

632   Many Bayesian studies dealing with the age of the angiosperms have tested the sensitivity of

633   molecular dates to different prior assumptions or partitioning schemes (Foster *et al.*, 2016;

634   Barba-Montoya *et al.*, 2018). However, other authors have directly investigated systematic

635   biases that could lead to overestimation of the age of the angiosperms. Beaulieu *et al.* (2015)

636   used a simulation approach to detect potential biases created by molecular rate heterogeneity

637   linked to habit (herbaceous vs. woody), as well as by the diversified sampling strategy

638   necessarily employed in such a large group. Their results demonstrated that even for sequences

639   generated on a simulated tree of angiosperms with a young crown-group age (140 mya), relaxed-

640 clock methods tended to overestimate the age of the crown group by as much as 70 my when

641 high-rate, herbaceous clades are present near the base of the group. More puzzlingly, the age of

642 the crown angiosperms was overestimated by 50 my even when simulations were conducted

643 under favorable conditions for relaxed-clock methods.

644

645 Another explanation for this perplexing phenomenon was offered by Brown & Smith (2018),

646 who identified a substantial issue with the implementation of node priors: the interaction

647 between the many different user-defined priors and the topology generated effective priors that

648 pushed the ages towards a much older origin of crown-group angiosperms than expected from

649 the user-specified priors.

650

651 These methodological and biological complications have been identified in placental mammals,

652 where the fossil record suggests an explosive radiation in the Paleocene and only stem relatives

653 are known from the Cretaceous, but molecular analyses place the radiation well back in the Late

654 Cretaceous. In this case, Phillips & Fruciano (2018) identified a connection between the use of

655 calibrations at the base of clades that show parallel shifts towards slow molecular rates (primates,

656 proboscidians) and older inferred ages for crown placentals. Two clades used for calibration in

657 angiosperms, Proteales and Fagales, may represent similar cases, since they both have unusually

658 short branches on molecular phylograms.

659

660 These considerations could mean that the tempo and mode of molecular evolution during the

661 origin and early radiation of the angiosperms are extremely hard to model. A deeper

662 investigation of the implications of fossil-informed ages for the mode of molecular evolution in

663 angiosperms could provide novel insights not only on the time of their origin, but also on

664 mechanisms acting at the molecular level during their radiation.

665

666 **V.   Conclusions**

667

668 This survey reaffirms the view that stratigraphic and morphological patterns in the Cretaceous

669 angiosperm record are difficult to reconcile with molecular dating analyses that place the origin

670 of the group long before the Cretaceous. Reports of pre-Cretaceous angiosperms do not offer

671 serious support for older molecular dates, and most are clearly erroneous. These results, like

672 those involving other taxa such as placental mammals (Phillips & Fruciano, 2018), underline the

673 need to investigate whether current molecular methods have inherent biases that are responsible

674 for conflicts of this type with the fossil record.

675

676 The Cretaceous record permits and may even favor some Jurassic diversification of the

677 angiosperms, and the nearly universal molecular support for a pre-Cretaceous origin should give

678 pause to a literal reading of the known record. It would be unwarranted to dismiss scenarios in

679 which low-diversity ANITA-grade angiosperms were ecologically and geographically restricted

680 in the Jurassic, e.g., if they grew in wet tropical understory habitats like woody members of the

681 ANITA grade (Feild *et al.*, 2004). In this case, the observed rise of reticulate monosulcate pollen

682 beginning in the Valanginian might mark the radiation of mesangiosperms. However, the amount

683 of pre-Cretaceous diversification implied by earlier Jurassic, Triassic, or Permian dates would

684 conflict with the Cretaceous record, in which successive new pollen types appear in the order of

685 evolution inferred from molecular phylogenetic analyses, but much later than predicted by

686 molecular dating.

687

688 Our review demonstrates that the fossil record provides what appears to be fundamental evidence

689 on the timescale and pattern of the origin and early evolution of angiosperms. This underlines the

690 continued importance of expertise in paleobotany and related fields. Many of the erroneous

691 interpretations of pre-Cretaceous fossils discussed here are due to misunderstandings of basic

692 plant morphology. From the viewpoint of molecular dating alone, paleobotanical expertise is

693 pivotal for successful calibration, especially now that the incorporation of fossil information

694 using well-curated morphological matrices is becoming common practice in the broader field

695 (Gavryushkina *et al.*, 2017). Furthermore, discovery of pre-Cretaceous crown-group angiosperm

696 fossils would confirm molecular evidence that angiosperms are older than their currently

697 accepted record, but recognition of angiosperm stem relatives could be vastly more significant

698 for understanding the origin of angiosperms and their distinctive features. Thus better evidence

699 on venation or cuticle of leaves such as *Phyllites* from the Stonesfield Slate or association of

700 Crinopolles pollen with other plant organs could result in major breakthroughs in angiosperm

701 paleobotany. However, full use of this information would require a broad and deep perspective

702 on plant morphology, anatomy, and taphonomy.

703

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705

712

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Supplementary information captions

Methods S1: Methods for our reconstruction of Lineages-through-time producing different kinds of pollen used in Fig. 4.

Notes S1: Description and reinterpretation of supposed pre-Cretaceous angiosperms.

Table S1: Taxa coded for generating Fig. 4 and sources of the data.

Figure legends

Fig. 1. Timescale, simplified dated molecular phylogeny of angiosperms (based on data of Magallón *et al.*, 2015), and noteworthy Cretaceous angiosperm pollen types and possible pre-

1099   Cretaceous relatives placed at their level of appearance (most Cretaceous types continue into

1100   younger beds). Diagrammatic sketches of fossil pollen types in polar view (sizes of pollen grains

1101   and sculpture not to scale): (a) Triassic pollen of Hochuli & Feist-Burkhardt (2013); (b)

1102   Crinopolles group; (c) Valanginian-Hauterivian reticulate monosulcate; (d) *Tucanopollis*; (e)

1103   *Clavatipollenites*; (f) *Stellatopollis*; (g) *Similipollis* (dotted line indicates proximal area of fine

1104   sculpture); (h) *Afropollis*; (i) *Liliacidites*; (i) *Walkeripollis* tetrad; (k, l) reticulate tricolpates

1105   (*Tricolpites*, *Rousea*); (m) striate tricolpate (*Striatopollis*); (n) tricolporoidate (equatorial view);

1106   (o) smooth prolate tricolporate; (p) smooth triangular tricolporate; (q) Normapolles group

1107   (*Complexiopollis*); (r) *Triorites africaensis*. Gray arrows indicate delayed general appearance of

1108   tricolpates in Southern Laurasia. Tri: Triassic; Jur: Jurassic; Ber: Berriasian; Val: Valanginian;

1109   Hau: Hauterivian; Bar: Barremian; Apt: Aptian; Alb: Albian; Cen: Cenomanian.

1110

1111   **Fig. 2.** Geographic and migrational patterns in the early angiosperm record, illustrated by

1112   paleogeographic maps for four intervals in the Early Cretaceous

1113   (http://www.odsn.de/odsn/services/paleomap/paleomap.html), with locations of selected

1114   geological sequences containing early angiosperm pollen (see section on "Temporal and spatial

1115   patterns in the pollen record" for discussion of selection criteria). Symbols indicate well-studied

1116   palynofloras with no reported angiosperm pollen, presence of monosulcate angiosperm pollen

1117   only, and presence of tricolpate (eudicot) pollen (as well as angiospermous monosulcates, except

1118   in Arctic Canada). When symbols are shown only for younger horizons, this indicates a lack of

1119   older sediments (e.g., below the Potomac Group) or insufficient palynological study of older

1120   beds (e.g., Portugal). Ages for base maps: (a) 129.4 Ma (Hauterivian-Barremian boundary); (b)

1121   125 Ma (Barremian-Aptian boundary); (c) 113 Ma (Aptian-Albian boundary); (d) 100.5 Ma

1122   (Albian-Cenomanian boundary).

1123

1124   Data for Arctic Canada (Sverdrup Basin, Ellef Ringnes and Ellesmere Islands): Brenner (1976),

1125   Galloway *et al.* (2012); western Canada plains (Alberta, Saskatchewan, Manitoba): Norris

1126   (1967), Playford (1971), Singh (1975); Potomac Group, eastern USA (Delaware, Maryland,

1127   Virginia): Doyle & Robbins (1977); England (Wealden and overlying marine units, southern

1128   England): Kemp (1968), Laing (1975), Hughes (1994); Portugal (Lusitanian and Algarve

1129   Basins): Heimhofer *et al.* (2007); Italy (southern Tuscany): Trevisan (1988); Israel: Brenner

1130 (1996); Egypt (Mersa Matruh, Dakhla Oasis): Schrank (1983, 1992), Penny (1991), Ibrahim

1131 (2002), Schrank & Mahmoud (2002); northeastern Brazil (Recôncavo-Tucano and Sergipe-

1132 Alagoas Basins): Regali & Viana (1989); Gabon/Congo (northern Gabon and Republic of the

1133 Congo): Doyle *et al.* (1977, 1982), Doyle (1992); northern Patagonia, Argentina (Neuquén

1134 Province): Archangelsky *et al.* (2009); southern Patagonia, Argentina (Santa Cruz Province):

1135 Archangelsky *et al.* (2009), Llorens & Perez Loinaze (2016), Perez Loinaze *et al.* (2016);

1136 Antarctica (James Ross Island, Antarctic Peninsula): Dettmann & Thomson (1987); Queensland,

1137 Australia (Eromanga and Surat Basins): Burger (1993); Victoria, Australia (Otway Basin):

1138 Dettmann (1973, 1986), Korasidis *et al.* (2016). Val: Valanginian; Hau: Hauterivian; Bar:

1139 Barremian; Apt: Aptian; Alb: Albian.

1140

1141 **Fig. 3.** Time of appearance (yellow symbols) and persistence (colored lines) of monosulcate

1142 (blue) and tricolpate (purple) angiosperm pollen plotted against paleolatitude, based on the data

1143 summarized in Fig. 2. For simplicity, paleolatitudes are based on positions of localities at the

1144 Aptian-Albian boundary (113 Ma, Fig. 2c); in some areas, particularly Australia and Antarctica,

1145 localities shift considerably in paleolatitude through time (cf. Fig. 2), but their early Albian

1146 latitudinal positions are close to those when each of the pollen classes appears. In England and

1147 the Potomac sequence, isolated earlier occurrences of tricolpate pollen (as opposed to consistent

1148 presence in most samples) are indicated by tricolpate symbols superimposed on the blue line.

1149 Tri: Triassic; Jur: Jurassic; Ber: Berriasian; Val: Valanginian; Hau: Hauterivian; Bar: Barremian;

1150 Apt: Aptian; Alb: Albian; Cen: Cenomanian.

1151

1152 **Fig. 4.** Comparison of temporal changes in diversity of lineages with pollen belonging to major

1153 classes predicted by a dated molecular tree and observed in the Early Cretaceous fossil record.

1154 Blue indicates sulcate (including monosulcate and derived pollen types, such as monoporate and

1155 sulculate); purple: colpate (including tricolpate, hexacolpate, and other presumably derived

1156 types); yellow: colporate (including tricolporate, tetracolporate, etc.); green: inaperturate; black:

1157 porate (including triporate, pantoporate, but not monoporate).

1158

1159 Left, predicted number of lineages through time based on the data set of Magallón *et al.* (2015)

1160 analyzed without the Early Cretaceous constraint on the angiosperm crown node. For sources of

1161   pollen data and methods, see Supporting Information. Pie diagrams show the relative

1162   probabilities of the different states at the reconstructed node; their position on the x-axis

1163   corresponds to the number of nodes at a given horizon that share the same reconstructed state

1164   weighted by its probability (see Supporting Information for details).

1165

1166   Right, curves of observed diversity of sulcate, colpate, and colporate angiosperm pollen

1167   "species" through time in three geological sections. Numbers at each horizon represent the

1168   number of species of the pollen class whose observed ranges pass through the horizon, not the

1169   number of species in any one sample. Sources of data: Egypt, Mersa Matruh 1 well, fig. 8 of

1170   Penny (1991), not including *Afropollis*; Portugal, Luz section (Algarve), fig. 9 of Heimhofer *et*

1171   *al.* (2007); Potomac Group, Delaware City wells D12 and D13 (Delaware), fig. 4 of Doyle &

1172   Robbins (1977). Numbers of species may not be directly comparable between sections due to the

1173   use of SEM by Penny (1991) vs. light microscopy by Heimhofer *et al.* (2007) and Doyle &

1174   Robbins (1977), different levels of attention to fine differences among pollen types, and other

1175   factors. The mid-Aptian peak of monosulcates in Egypt may be exaggerated because of Penny's

1176   intensive study of the monosulcate *Pennipollis* group; declines in diversity at the top of the

1177   Egyptian and Portuguese sections may relate to decreasing sample richness and/or less intensive

1178   study. Dashed lines show downward extensions of monosulcate angiosperms within the same

1179   phytogeographic province, with the line below the curve for Egypt (Northern Gondwana) based

1180   on data from Italy (Trevisan, 1988) and Israel (Brenner, 1996), and the line below the curve for

1181   Portugal (Southern Laurasia) based on the Wealden of England (Hughes, 1994). The two breaks

1182   in curves in the Potomac sequence correspond to depositional hiatuses, the lower of which

1183   reflects thinning of the Aptian portion of the Potomac Group in Delaware. The later appearance

1184   of tricolpates in Portugal and the Potomac relative to Egypt illustrates their delayed northward

1185   migration across the Tethys (cf. Figs. 2, 3). Tri: Triassic; Jur: Jurassic; Ber: Berriasian; Val:

1186   Valanginian; Hau: Hauterivian; Bar: Barremian; Apt: Aptian; Alb: Albian; Cen: Cenomanian.

1187

1188   **Fig. 5.** Possible pre-Cretaceous angiosperms or angiosperm relatives. (a-d) Crinopolles pollen,

1189   Chinle Formation, Late Triassic, Arizona (Doyle & Hotton, 1991); (a, b) light micrographs, two

1190   focal levels; (c) scanning electron micrograph, proximal view; (d) transmission electron

1191   micrograph of flattened grain, e = endexine. (e, f) *Phyllites* sp. of Seward (1904), Stonesfield

1192 Slate, Middle Jurassic, England (Cleal & Rees, 2003), part and counterpart, courtesy of C. J.

1193 Cleal and The Palaeontological Association. Bars: (a, b) 10 µm; (c) 5 µm; (d) 1 µm; (e, f) 10

1194 mm.

1195

1196 **BOXES**

1197

1198 **Box 1: Definitions of phylogenetic and palynological terms.**

1199

1200 Crown group: the most recent common ancestor of a living clade and all its descendants, both

1201 living and fossil. All clades recognized in molecular analyses are crown groups.

1202

1203 Stem lineage: the evolutionary line connecting a crown group with its common ancestor with the

1204 most closely related living group (sister group).

1205

1206 Stem relative: an extinct group on or attached to the stem lineage.

1207

1208 Monosulcate: with a single elongate furrow-like polar aperture (sulcus) of thinner exine for

1209 pollen tube germination; the polar axis is defined by an imaginary line running through the

1210 center of the pollen grain and the center of the meiotic tetrad in which it was formed (see

1211 accompanying sketch of pollen tetrad and Fig. 1a-g).

1212

1213 Tricolpate: with three elongate furrow-like apertures (colpi, singular colpus) for pollen tube

1214 germination running along lines of longitude (relative to the polar axis as defined above; see

1215 accompanying sketch of pollen tetrad and Fig. 1k-m).

1216

1217 Tricolporate: with three colpi plus an internally differentiated pore or os (plural ora) in the

1218 middle of each colpus. The resulting apertures are described as compound (see Fig. 1n-p).

1219

1220 Triporate: with three round apertures. Pores may be simple or compound (with differentiated

1221 inner and outer apertures; see Fig. 1q, r).

1222

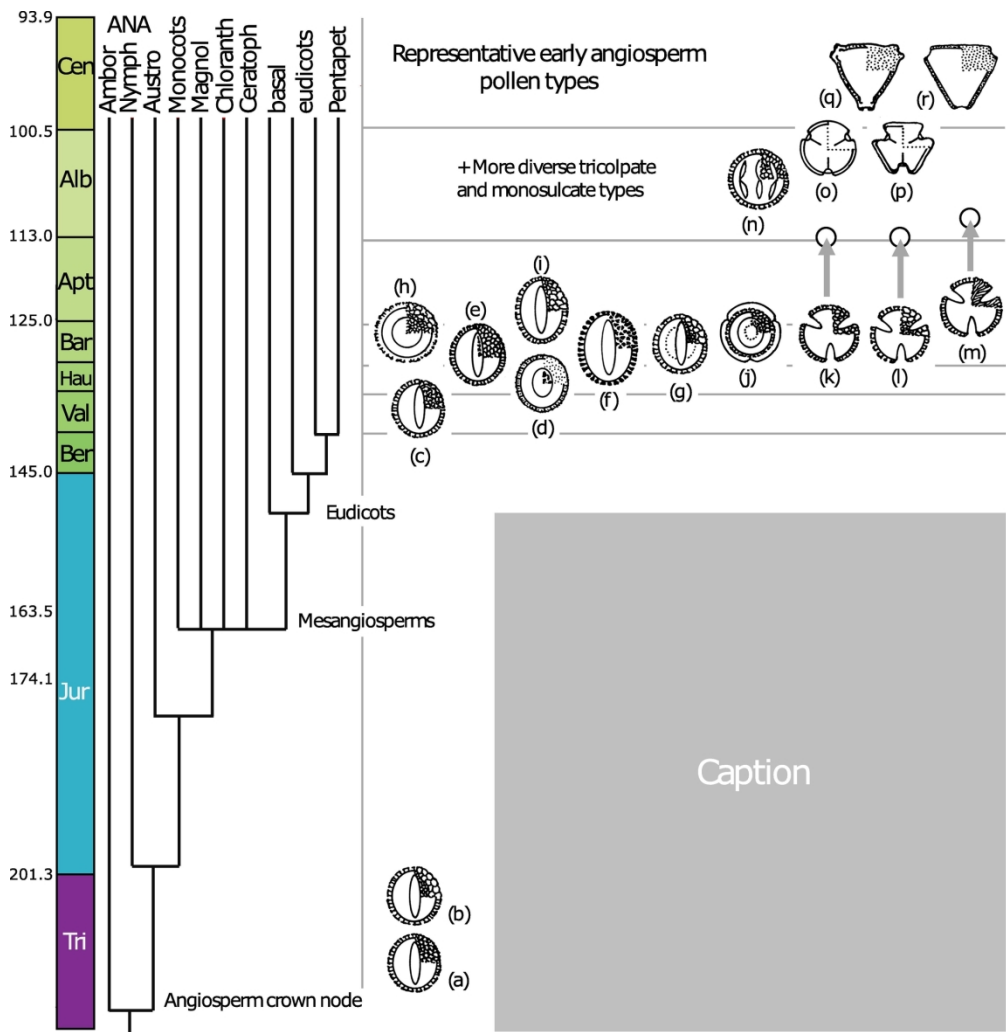1223   Pantoporate, periporate, polyforate: with numerous round apertures scattered over the surface of

1224   the grain.

1225

1226   Disulculate, zonasulculate: with two furrows or one ring-like furrow, respectively, on or parallel
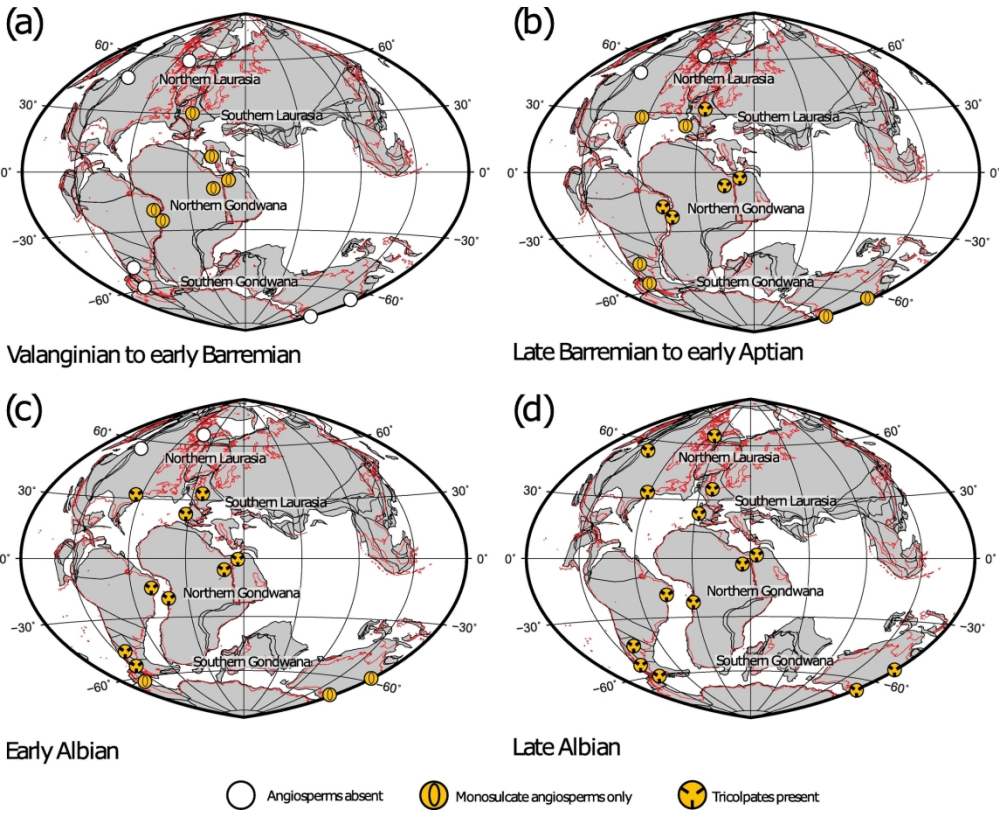
1227   to the equator.

1228

1229   Inaperturate: with no differentiated aperture (and usually a thin exine, in which the pollen tube

1230   can germinate at any point).

1231

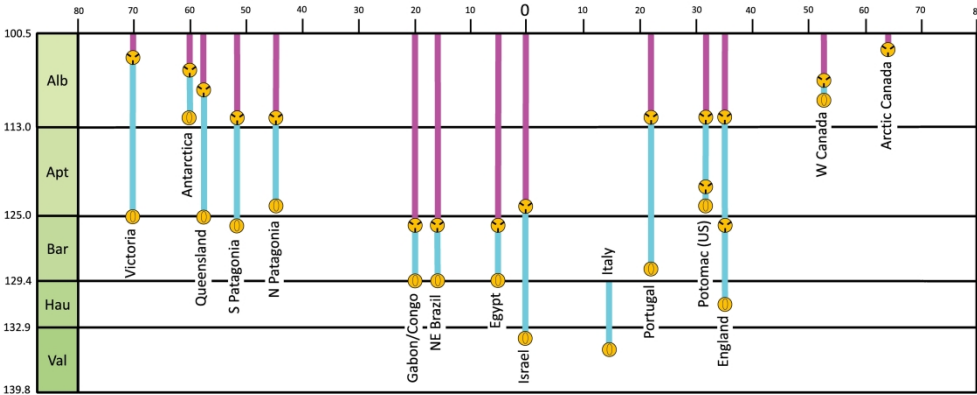1232   **Box 2: Aquatic origin of angiosperms.**

1233

1234   Coiffard *et al.* (2012) interpreted the abundance of aquatic angiosperms such as *Montsechia*,

1235   Nymphaeales, and *Archaefructus* in Barremian-Aptian lacustrine deposits as evidence that the

1236   angiosperms were originally aquatic. There is no question that aquatic habitats were among the

1237   first where angiosperms were abundant, but this does not necessarily mean they originated there.

1238   The position of aquatic clades in molecular phylogenies suggests rather that the aquatic habit was

1239   a specialization that arose in several early lines, namely Nymphaeales, *Ceratophyllum*, *Nelumbo*

1240   among eudicots, and monocots, in which the earliest-diverging line, *Acorus*, and basal members

1241   of the second line, Alismatales, are marsh plants. These lines are nested among groups of

1242   terrestrial plants with normal woody stems (*Amborella*, Austrobaileyales, Chloranthaceae,

1243   Magnoliidae). The stem anatomy of these terrestrial groups is difficult to explain if they were

1244   derived from aquatic ancestors, in which secondary growth is highly reduced or absent (Feild &

1245   Arens, 2007). Furthermore, given the wide geographic distribution of modern aquatic plants and

1246   the fact they usually grow in sites of sedimentary deposition, it seems difficult to explain how

1247   angiosperms could originate long before the Cretaceous and remain undetected if they were

1248   originally aquatic. Together, these arguments suggest that a better explanation for the Barremian-

1249   Aptian abundance of aquatics may be the higher probability of preservation of plants in

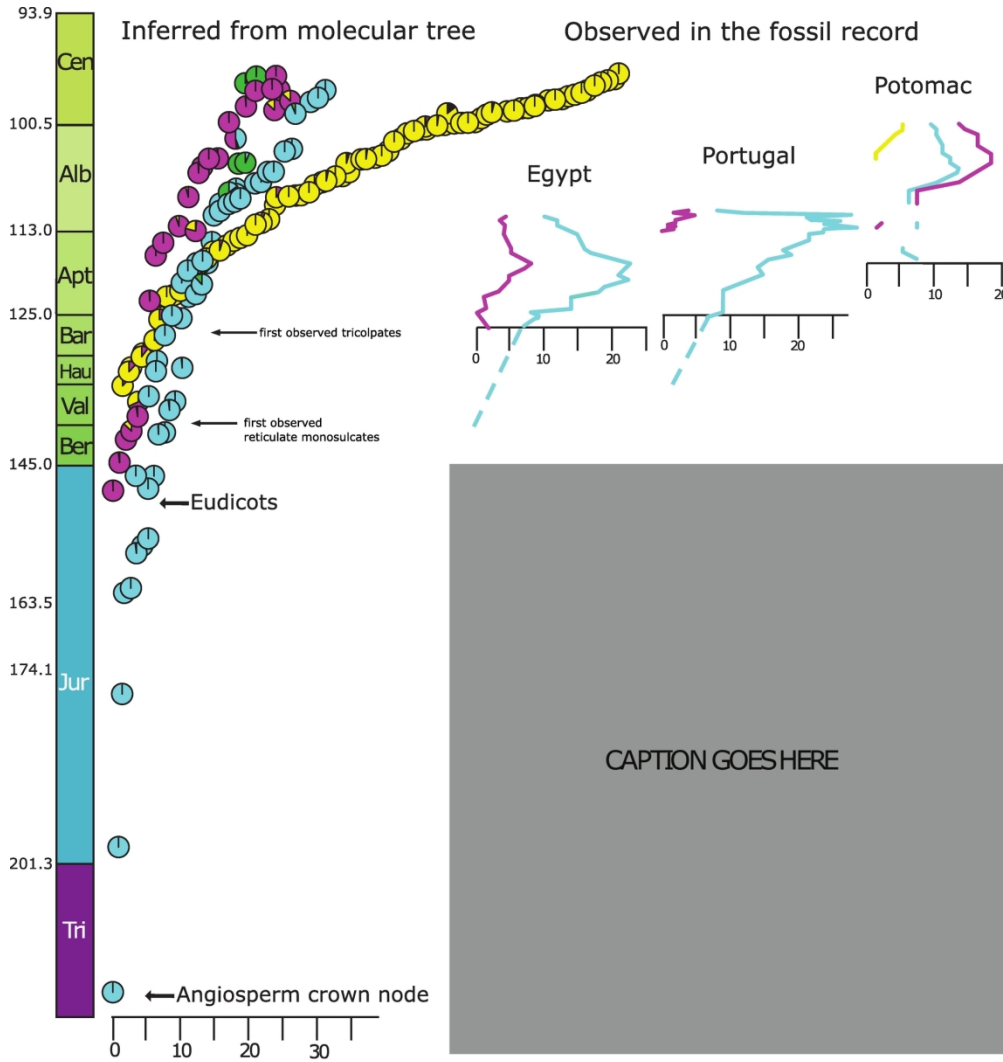1250   lacustrine sedimentary environments than in contemporaneous drier habitats.

1251

1252

1253

Representative early angiosperm pollen types

+ More diverse tricolpate and monosulcate types

184x188mm (300 x 300 DPI)

(a) Valanginian to early Barremian

(b) Late Barremian to early Aptian

(c) Early Albian

(d) Late Albian

○ Angiosperms absent   ◍ Monosulcate angiosperms only   ☢ Tricolpates present

182x146mm (300 x 300 DPI)

355x162mm (300 x 300 DPI)

186x195mm (300 x 300 DPI)