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Fossil fern rhizomes as a model system for exploring epiphyte community structure across geologic time: Evidence from Patagonia

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Background. A wealth of data on the networks of ecological interactions present in the modern biota can be readily obtained, due to the ease of unlimited access to the living organisms. In contrast, understanding of such interactions in ecosystems of the geologic past is incomplete. Specifically, in past terrestrial ecosystems we know comparatively little about plant biotic interactions besides saprotrophy, herbivory, mycorrhizal associations, and oviposition. Due to taphonomic biases, epiphyte communities are particularly rare in the fossil record, despite their prominence in modern ecosystems. Accordingly, little is known about how epiphyte communities have changed across geologic time. Here, we describe a tiny in situ fossil epiphyte community that sheds light on plant-animal and plant-plant interactions more than 50 million years ago. **Methods.** A single silicified *Todea* rhizome from a new locality of the early Eocene (ca. 52 Ma) Tufolitas Laguna del Hunco (Patagonia, Argentina) was studied in serial thin sections using light microscopy. The community of organisms colonizing the tissues of the rhizome was characterized by identifying the organisms, as well as mapping and quantifying their distribution. A 200 x 200 μm grid was superimposed onto the rhizome cross section, and the colonizers present at each node of the grid were tallied. **Results.** Preserved in situ, this community offers a rare window onto aspects of ancient ecosystems usually lost to time and taphonomic processes. The community is surprisingly diverse and includes the first fossilized leafy liverworts in South America, also marking the only fossil record of leafy bryophyte epiphytes outside of amber deposits; several types of fungal hyphae and spores; microsclerotia with possible affinities in several ascomycete families; and oribatid mite coprolites. **Discussion.** The community associated with the Patagonian rhizome enriches our understanding of epiphyte communities in the distant past and adds to a growing body

of literature on osmundaceous rhizomes as important hosts for component communities in ancient ecosystems, just as they are today. Because osmundaceous rhizomes represent an ecological niche that has remained virtually unchanged over time and space and are abundant in the fossil record, they provide a paleoecological model system that could be used for exploring epiphyte community structure through time.

1   **Fossil fern rhizomes as a model system for exploring epiphyte community structure across**

2   **geologic time**: **Evidence from Patagonia**

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17 **Abstract**

18 **Background.**

19 A wealth of data on the networks of ecological interactions present in the modern biota can be

20 readily obtained, due to the ease of unlimited access to the living organisms. In contrast,

21 understanding of such interactions in ecosystems of the geologic past is incomplete.

22 Specifically, in past terrestrial ecosystems we know comparatively little about plant biotic

23 interactions besides saprotrophy, herbivory, mycorrhizal associations, and oviposition. Due to

24 taphonomic biases, epiphyte communities are particularly rare in the fossil record, despite their

25 prominence in modern ecosystems. Accordingly, little is known about how epiphyte

26 communities have changed across geologic time. Here, we describe a tiny in situ fossil epiphyte

27 community that sheds light on plant-animal and plant-plant interactions more than 50 million

28 years ago.

29 **Methods.**

30 A single silicified *Todea* rhizome from a new locality of the early Eocene (ca. 52 Ma) Tufolitas

31 Laguna del Hunco (Patagonia, Argentina) was studied in serial thin sections using light

32 microscopy. The community of organisms colonizing the tissues of the rhizome was

33 characterized by identifying the organisms, as well as mapping and quantifying their distribution.

34 A 200 x 200 μm grid was superimposed onto the rhizome cross section, and the colonizers

35 present at each node of the grid were tallied.

36 **Results.**

37 Preserved in situ, this community offers a rare window onto aspects of ancient ecosystems

38 usually lost to time and taphonomic processes. The community is surprisingly diverse and

39 includes the first fossilized leafy liverworts in South America, also marking the only fossil

40 record of leafy bryophyte epiphytes outside of amber deposits; several types of fungal hyphae

41 and spores; microsclerotia with possible affinities in several ascomycete families; and oribatid

42 mite coprolites.

43 **Discussion.**

44 The community associated with the Patagonian rhizome enriches our understanding of epiphyte

45 communities in the distant past and adds to a growing body of literature on osmundaceous

46 rhizomes as important hosts for component communities in ancient ecosystems, just as they are

47 today. Because osmundaceous rhizomes represent an ecological niche that has remained

48   virtually unchanged over time and space and are abundant in the fossil record, they provide a

49   paleoecological model system that could be used for exploring epiphyte community structure

50   through time.

51

52   **Introduction**

53   In the modern biota, direct access to organisms has revealed significant parts of their

54   networks of ecological interactions. In contrast, understanding of such interactions is incomplete

55   in ecosystems of the geologic past. Specifically, in past terrestrial ecosystems we know

56   comparatively little about plant biotic interactions besides saprotrophy, herbivory, mycorrhizal

57   associations, and oviposition (DiMichele et al., 1992; Labandeira & Currano, 2013; Taylor et al.,

58   2015). Here, we investigate a complex community of organisms that lived in association with an

59   osmundaceous fern, preserved in Eocene rocks (ca. 52 Ma) of La Huitrera Formation,

60   Argentinean Patagonia. La Huitrera Formation hosts one of the most diverse Eocene floras

61   characterized to date (Wilf et al., 2003, 2005a), yet the interactions of plants in this flora with

62   other organisms are just beginning to be characterized (Wilf et al., 2005b). The fossil

63   community associated with the osmundaceous fern is surprisingly diverse and includes the first

64   fossil epiphytic liverworts known outside of amber deposits. Preserved in situ, this community

65   offers a rare window onto aspects of ancient ecosystems usually lost to time and taphonomic

66   processes. Such ecologically relevant aspects of community dynamics (abundance and diversity

67   of epiphytes and incidence of herbivory), typically unavailable for fossil associations, are

68   described here. Rather than describing in detail the biotic interactions between members of this

69   community, here we aim to provide an assessment of epiphyte community structure. We also

70   use a broad definition of epiphyte, which encompasses all organisms that live on a host plant.

71   Together, the fossils represent a tiny epiphyte community centered around a single host plant.

72

73   **Materials and Methods**

74   Geologic setting

75   The fossils described here come from a new site ca. 2.1 km south of the Chubut River

76   and 9.8 km due west of Piedra Parada in northwestern Chubut Province, Patagonian Argentina, S

77   42°39'20.60", W 70°13'22.20". The source strata belong to the Tufolitas Laguna del Hunco, an

78   early Eocene, volcaniclastic, caldera-fill lacustrine deposit of La Huitrera Formation that is

79   embedded in the Middle Chubut River Volcanic-Pyroclastic Complex (Aragón and Mazzoni,

80   1997). The new fossil site sits in the southern exposure area of the Tufolitas Laguna del Hunco,

81   ca. 24 km SSW of the well-known Laguna del Hunco fossil locality (Berry, 1925; Petersen,

82   1946; Wilf et al., 2003), which lies in the northeastern exposures of the same extensive, highly

83   fossiliferous unit. This is the first report of fossil plants from the southern exposures, although

84   the nearby Laguna Fría mammal assemblage potentially correlates to these strata (Tejedor et al.,

85   2009). In this southern area, an ignimbrite that caps the fossil lake bed exposures ca. 5 km east

86   of the new fossil site yielded an ^{40}Ar-^{39}Ar age on plagioclase of 49.26 ± 0.56 Ma (early Eocene,

87   Ypresian) in an unpublished thesis (Gosses, 2006; Gosses et al., 2006), directly providing a

88   minimum age for the osmundaceous rhizome. We note that this age has not been subsequently

89   vetted or revised for updated decay constants (Kuiper et al., 2008), but it is likely to be broadly

90   accurate because it lies in correct stratigraphic order relative to other dated samples from the

91   Eocene caldera system (Gosses, 2006; Gosses et al., 2006; Kuiper et al., 2008; Tejedor et al.,

92   2009).

93   At Laguna del Hunco (northeastern exposures), three ^{40}Ar-^{39}Ar ages from volcanic ashes

94   and two recorded paleomagnetic reversals, all from strata located within the main fossiliferous

95   section of the Tufolitas Laguna del Hunco, constrain the time of fossil deposition there to the

96   early Eocene as well (Wilf et al., 2003, 2005a). The most reliable radiometric age at Laguna del

97   Hunco, on sanidines from an ash taken from the middle of the most densely sampled

98   fossiliferous interval and analyzed in two different labs, is 52.22 ± 0.22 Ma (early Eocene,

99   Ypresian) following recalibration for modern decay constants (Wilf et al., 2003; Wilf et al.,

100   2005; Kuiper et al., 2008; Wilf, 2012; Wilf et al., 2017). Thus, the osmundaceous rhizome can

101   safely be considered Ypresian and in the age range of ca. 49.3 to perhaps 52.5 Ma. We prefer

102   the older end of this range because the dates from Laguna del Hunco, despite their ca. 24 km

103   geographic distance from the new fossil site, come from tuffs located within the Tufolitas

104   Laguna del Hunco, the same unit that holds the osmundaceous rhizome fossil. The dated

105   ignimbrite in the southern area (Gosses, 2006; Gosses et al., 2006) lies above that unit.

106   At Laguna del Hunco itself, the Tufolitas Laguna del Hunco host one of the most diverse

107   Eocene compression floras known (Wilf et al., 2003, 2005a). The flora has a robust Gondwanic

108   component displayed among its gymnosperm and angiosperm species, as described extensively

109   elsewhere; among the most striking occurrences are the well-preserved and abundant fossils of

110 *Agathis* (Araucariaceae) and *Eucalyptus* (Myrtaceae) (Wilf et al., 2013; Gondalfo et al., 2011;

111 Wilf et al., 2014).

112

113 The host fern

114   The host plant is a permineralized osmundaceous fern rhizome ca. 8 cm in diameter and

115 20 cm tall. This rhizome and associated sterile foliage collected from the same locality were

116 recently described as *Todea* cf. *amissa* M. Carvalho, a species initially described based on

117 compressions of sterile and fertile foliage from the northeastern exposures of Laguna del Hunco

118 (Carvalho et al., 2013; Bomfleur and Escapa, 2019). The two records of *Todea* in the Tufolitas

119 Laguna del Hunco comprise the only South American fossil or extant record of the genus (extant

120 in Australia, New Guinea, and southern Africa) (Carvalho et al., 2013).

121

122 Methods

123   The *Todea amissa* rhizome was studied in serial thin sections using light microscopy.

124 Photographs of whole thin sections were taken using a light box and a Canon EOS 70D Camera

125 fitted with a Canon 60mm macro lens, and were stitched together using Photoshop CC (Adobe,

126 San Jose, California, USA). All other micrographs were taken using a Nikon Coolpix E8800

127 digital camera mounted on a Nikon Eclipse E400 microscope and processed using Photoshop

128 CC. All specimens and preparations are housed in the collections of the Museo Paleontologico

129 Egidio Feruglio (MPEF), Trelew, Argentina. The distribution of colonizing organisms in fern

130 tissue was quantified by superimposing a 200 μm x 200 μm grid onto the cross section of the

131 rhizome (Fig. 1). At each intersection of the grid, we recorded the type of fern tissue and the

132 presence and type of colonizers. This yielded 3,820 data points for the entire rhizome cross

133 section. Of these, 252 data points included colonizing organisms (see Table 1).

134

135 **Results**

136 Epiphytic plants

137   More than 25 small leafy shoots are found, primarily along the outer perimeter on one

138 side of the rhizome, but also between leaf bases elsewhere along the rhizome (Fig. 1). The leafy

139 shoots are up to 3.75 mm long and 230-410 μm in diameter. They exhibit pinnate branching,

140 with branches > 200 μm long, diverging at 450-850 μm intervals (Fig. 2B-C). Stems are 30-180

141 μm in diameter, comprised entirely of isodiametric to oval parenchyma cells 10-22 μm across

142 and 55-78 μm long (Fig. 2B). Leaves are two-ranked and attached at 10-45 μm intervals (Fig.

143 2A). Incompletely preserved, they are at least 490 μm long, lack a midrib, and are inserted at

144 30-40° angles (Fig. 2A-B). Their thickness (7.5-12.5 μm) indicates that they are probably

145 unistratose.

146   Additionally, a small root was found in the detritus at the periphery of the rhizome (Fig.

147 1). The root is 0.7 mm in diameter and has a diarch protostele ca. 100 μm wide (Fig. 2D).

148 Secondary xylem with narrow (10-21 μm) tracheids (Fig. 2D) comprise ca. 75 % of the root;

149 some bark is also preserved (Fig. 2D).

150

151 Fungi

152   Fungal hyphae are abundant in highly degraded parts of the rhizome and in surrounding

153 plant detritus (Fig. 1, 2L). They fall into two types: (1) smaller, apparently aseptate hyphae 1.5-

154 2.0 μm in diameter; and (2) larger, septate hyphae 3.0-5.0 μm in diameter (Fig. 2L). The latter

155 have septa spaced at 21-22 μm; clamp connections were not observed.

156   Darkly pigmented, round to oval cerebriform microsclerotia are also abundant in highly

157 degraded parts of the rhizome and in the associated plant detritus (Fig. 1). The microsclerotia are

158 42-50 μm in diameter and composed of isodiametric to oval cells 4-12 μm in size (Fig. 2F).

159   Five other types of dispersed fungal reproductive structures are present in detritus

160 associated with the rhizome (Fig. 1, 2G-K). These reproductive structures are multicellular

161 (three to eight celled), uniseriate, more-or-less linear spores lacking obvious pores (Fig. 2G-K);

162 four of the five types are preserved with narrow stalks (Fig. 2G, 2H-K). Type one consists of

163 stalked, three-celled spores (Fig. 2G) ca. 15 μm long x 6 μm wide. The apical cell is rounded, 4

164 μm long x 6 μm wide. The middle cell is smaller, rectangular, 3 μm long x 6 μm wide. The

165 basal cell is >10 μm long and 6 μm wide, tapering basally into a stalk 4 μm wide. Type two

166 includes three celled, stalked spores roughly elliptical in shape, ca. 40 μm long and up to 16 μm

167 wide (Fig. 2K). The apical cell is shaped like a truncated ellipse, 18 μm long and 16 μm wide.

168 The subapical cell is rectangular, 11 μm long x 16 μm wide. The basal cell is trapezoidal, 6 μm

169 long and 13 μm wide apically, tapering to 6 μm basally. The stalk tapers to 4 μm. Type three

170 consists of elongate, stalked, 7- or 8-celled spores ca. 35 μm long and 6 μm wide (Fig. 2H).

171 Cells, except for the basal and apical ones, are rectangular, 3-5 μm long x 6 μm wide. The apical

172 cell is rectangular-trapezoidal and slightly smaller, 2 µm long x 5 µm wide. The basal cell is

173 also smaller, rectangular-trapezoidal, 3.5 µm long x 4 µm wide. The stalk tapers to 2 µm. Type

174 four is the most abundant fungal spore, three-celled, stalked and spatulate, ca. 25-30 µm long and

175 15 µm wide (Fig. 2J). The apical cell is round, 13-17 µm in diameter. The middle cell is small

176 and rectangular, 5-7 µm long x 7-8 µm wide. The basal cell is rectangular-trapezoidal, 8 µm

177 long and 7 µm wide apically, tapering to 5 µm basally. The stalk tapers to 3-4 µm. Type five

178 consists of slightly curved chains of five cells, ca. 38 µm long and 9 µm wide (Fig. 2I). The

179 apical cell is rounded, 8 µm long and 6 µm wide. The sub-apical cell is inflated, 7 µm long x 9

180 µm wide. The third cell is rectangular-trapezoidal, 7 µm long x 5 µm wide, tapering to 4 µm.

181 The fourth cell is rectangular, 6 µm long x 4 µm wide. The basal cell is square, 4 µm across.

182

183 Coprolites

184   Small, round to ovoid coprolites occur towards the periphery of the rhizome, in

185 excavations of the parenchymatous mesophyll, fiber band, and vascular tissue (Fig. 1, 2E).

186 Coprolites also occur externally to fern tissues, around highly degraded portions of the rhizome

187 (Fig. 1). They have smooth surfaces and are 23-260 µm in diameter, composed of angular cell-

188 wall fragments and opaque bodies (Fig. 2E).

189

190 Minute spherical structures

191   The degraded portions of the rhizome have groups of cells that are filled with small,

192 spherical structures 2-6 µm in diameter (Fig. 2M). These structures occur in cells of all tissue

193 types (parenchymatous leaf base mesophyll, fiber band, and vascular tissue) (Table 1).

194

195 **Discussion**

196 Taxonomic affinities of epiphytes

197

198 *Small epiphytic plants*

199   The small size of these plants and their lack of conducting tissues indicate that they are

200 bryophytes. The only bryophyte group that combines pinnately branched gametophytes with

201 two-ranked leaves that are unistratose, lack a midrib, and are inserted at wide angles to the stem

202 are leafy liverworts (Schofield, 1985). The incomplete preservation of the leaves, which

203 typically provide taxonomically informative characters among liverworts, precludes a narrower

204 systematic placement of these plants.

205

206 *Root*

207   The diarch primary xylem and high proportion of secondary xylem, lacking vessels, are

208 features typical of gymnosperms (Esau, 1965).

209

210 *Fungi*

211   The microsclerotia documented here are similar in size and morphology to the

212 cerebriform microsclerotia described in the roots of *Eorhiza arnoldii* Robison et Person from the

213 Eocene of Canada, which were attributed to dark septate endophytes belonging to a lineage of

214 dematiaceous ascomycetes (Klymiuk, Taylor & Taylor, 2013b).

215   Type one spores compare in overall morphology to smaller members of the dispersed

216 fossil spore genus *Diporicellaesporites* Elsik, especially *D. minisculus* Sheffy et Dilcher, but the

217 pores diagnostic of this genus (Kalgutkar & Jansonius, 2000) are not observable in the

218 Argentinean material. Type two and four spores are comparable to species of the dispersed spore

219 genus *Brachysporites* Lange et Smith, whose multicellular, usually spatulate spores resemble

220 conidia of the extant dematiaceous ascomycete genus *Brachysporium* Saccardo (Kalgutkar &

221 Jansonius, 2000; Taylor, Krings & Taylor, 2015). Within *Brachysporites*, type two spores are

222 most similar to *B. atratus* Kalgutkar, while type four spores are most similar to *B. pyriformis*

223 Lange et Smith (Kalgutkar & Jansonius, 2000). Type three spores are comparable to conidia of

224 the extant magnaporthaceous ascomycete *Clasterosporium* Schwein. (Kalgutkar & Jansonius,

225 2000); the extinct *C. eocenicum* Fritel et Viguier is especially similar to our type three spores,

226 although the latter are slightly smaller. Type five spores are comparable to the conidia of the

227 extant pleosporaceous ascomycete *Curvularia* Boedijn based on their size, curved shape, and

228 inflated subapical cell (Elsik, 1993).

229   Overall, the fungal reproductive structures documented on the *Todea* rhizome are

230 comparable with those of several ascomycete lineages, including Dematiaceae (microsclerotia

231 and two of the spore types), Magnaporthaceae, and Pleosporaceae (Elsik, 1993; Kalgutkar &

232 Jansonius, 2000; Klymiuk, Taylor & Taylor, 2013b). Septate hyphae lacking clamp connections

233 frequently found in the vicinity of these reproductive structures are consistent with ascomycete

234 affinities. Given that all this fungal material was found in detritus or very degraded plant

235 material (Fig. 1), these fungi, which were a component of the epiphyte community, were

236 probably saprotrophs, rather than parasites or endophytes.

237

238 *Coprolites*

239 Based on their size, shape and texture, the excavations and coprolites were probably

240 produced by oribatid mites (Labandeira, 1998; Kellogg & Taylor, 2004; McLoughlin and

241 Bomfleur, 2016).

242

243 *Small spherical structures*

244 Their perfectly circular shape, tendency to completely fill cells, and variable size indicate

245 that these structures are not microorganisms and are probably not of cellular nature. Instead,

246 they probably represent a type of cell content degradation and aggregation due to the

247 fossilization processes, also seen in the Early Devonian Rhynie chert plants (Michael Krings,

248 personal comm., 2017).

249

250 Distribution patterns

251 The distribution of colonizing organisms and differential preservation of central vs.

252 peripheral tissues in the *Todea* rhizome indicate that parts of this rhizome were probably alive

253 prior to fossilization. Consistent with this interpretation, vascular tissues near the center of the

254 rhizome are well-preserved and are neither populated by colonizers (Fig. 1) nor degraded (Figure

255 3A). However, some of the peripheral leaf bases are highly degraded, surrounded by organic

256 detritus (Figure 3A), and richly populated with colonizers (Fig. 1). The leaf bases on one side of

257 the rhizome are particularly degraded, and this region is most densely colonized by epiphytic

258 organisms (Fig. 1). Some leaf bases in this region contain coprolite-filled galleries large enough

259 to adversely affect the physiological functions and structural integrity of these leaves (Figure

260 3B). Together, these observations indicate that the most degraded and heavily colonized

261 peripheral leaf bases were probably dead at the time of fossilization, whereas the stem and more

262 centrally-located, less degraded leaf bases were probably alive. This distribution of degraded

263 and living tissues is not surprising, since the rhizomes of living Osmundaceae are often

264 surrounded by a mantle of degraded and richly colonized dead leaf bases (Fig. 3C).

265   The fossil *Todea* rhizome exhibits dense colonization by a diverse community of

266   epiphytes, which cover it in several kinds of life (Fig. 1), just like extant osmundaceous rhizomes

267   (Fig. 3C). The distribution and frequency of each kind of organism associated with the rhizome

268   by tissue type (Fig. 2N-O; Table 1) show that most associated organisms are much more

269   abundant in the more degraded region of the rhizome (Fig. 1). Liverworts and fungi in detritus

270   are found primarily external to the fern tissues, and secondarily within some of the most

271   degraded tissues near the periphery of the rhizome (Fig. 1, 2N-O). Coprolites also occur in all

272   types of tissue, as well as externally to some of the most degraded leaf bases, indicating that the

273   arthropods that produced them did not have strong preference for lignified or parenchymatous

274   tissues (Fig. 1, 2N-O).

275

276   Comparison with the Jurassic community associated with *Osmunda pulchella*

277   A community of organisms similar to that of the *Todea* rhizome has been described

278   associated with an exceptionally well preserved *Osmunda pulchella* Bomfleur, G. Grimm et

279   McLoughlin rhizome from the Jurassic of Sweden (Bomfleur, McLoughlin & Vajda, 2014;

280   McLoughlin & Bomfleur, 2016). Like the Patagonian community, this Jurassic community

281   included fungi, oribatid mites (coprolites) and epiphytic plants. However, in the case of the

282   *Osmunda pulchella* community, the epiphytic plants are exclusively vascular (lycopsids and

283   ferns), which may indicate that bryophytes had not yet evolved the epiphytic habit during the

284   Jurassic. Additionally, fungal material is more abundant and diverse in the Patagonian rhizome,

285   probably correlated with higher proportions of decomposed tissues. The richness of the

286   communities associated with both of these osmundaceous rhizomes suggests that other

287   permineralized fern rhizomes are likely to yield diverse communities of associated organisms.

288

289   Significance of the leafy liverwort fossils

290   Given the sparse fossil record of liverworts (Oostendorp, 1987; Tomescu, 2016;

291   Heinrichs et al., 2018; Tomescu et al., 2018), it is not surprising that these tiny epiphytes

292   represent the first report of fossil leafy liverworts from South America. *Marchantites hallei*

293   Lundblad (Lundblad, 1955), a thalloid liverwort from the Early Cretaceous of Argentina, is the

294   only other unequivocal fossil liverwort known from South America (Oostendorp, 1987; Tomescu

295   et al., 2018). However, three additional compression fossils from Bolivia and Argentina that

296   lack cellular detail have also been compared with thalloid liverworts (Jain and Delevoryas, 1967;

297   Cardozo and Iannuzzi, 2004; Coturel and Savoretti, 2018; Tomescu et al., 2018).

298   The liverworts described here are also the first epiphytic leafy gametophytes documented

299   in the fossil record outside of amber deposits [see Grolle and Meister (2004), Frahm (2010), and

300   Heinrichs et al. (2018) for reviews of bryophytes preserved in amber]. All other non-amber

301   fossils of epiphytic bryophytes are moss protonemata described on angiosperm leaves

302   (Mägdefrau, 1956; Selkirk, 1974; Barclay et al., 2013).

303

304   Importance of understanding epiphyte communities in fossil biotas

305   Today, rich epiphyte communities are found in several biomes, including boreal forests

306   (McCune, 1993), tropical lowland rainforests (Cornelissen and Ter Steege, 1989), and tropical

307   montane forests (Wolf, 1993a,b). In these ecosystems, epiphyte communities provide critical

308   ecological services, including soil production within forest canopies (Enloe et al., 2006),

309   increased nutrient input (Coxson and Nadkarni, 1995), and increased water storage (Pócs, 1980;

310   Vaneklaas and van Ek, 1990; Pykper et al., 2005). Thus, epiphyte communities significantly

311   influence the ecology of their host plants. The makeup of epiphyte communities is diverse in the

312   modern biota and co-varies dramatically with forest composition. In boreal forests of Pacific

313   Northwest North America, lichens and mosses may dominate epiphyte communities (McCune,

314   1993), whereas bromeliads and orchids may dominate such communities in a mid-elevation

315   rainforest of central Mexico (Hietz and Hietz-Seifert, 1995). The evolution of the deeply

316   divergent epiphyte communities in these biomes is critical in understanding the ecology and

317   evolutionary history of the forests themselves. However, our understanding of epiphyte

318   community composition in the distant past is poor and based on a small number of examples

319   (e.g., Rothwell, 1991; Rössler, 2000; McLoughlin & Bomfleur, 2016).

320   Knowledge of complex epiphyte communities in fossil biotas, including detailed insight

321   into component communities like those of this Patagonian rhizome, is needed to paint a more

322   complete picture of life in the geologic past and contextualize the evolution of epiphyte

323   communities. Past epiphyte communities probably provided the same kinds of ecosystem

324   services as those of the modern biota because these functions are independent of epiphyte

325   community structure. Thus, attempts to understand the ecology of these fossil biotas without

326   epiphytes ignore a critical component of the ecosystem. If we wish to understand the ecology of

327 past terrestrial environments, an understanding of epiphyte community structure is necessary.

328 Similarly, an understanding of ancient epiphyte communities is required to contextualize their

329 modern counterparts in an evolutionary framework (Gerhold et al., 2018).

330

331 Osmundaceous rhizomes as a model system for understanding epiphyte community structure

332   In principle, an appropriate host organism could provide a model system to track

333 epiphytes through geologic time, and from this we could determine when certain groups evolved

334 the epiphytic habit (e.g., modern leptosporangiate ferns, lycophytes, bryophytes, angiosperms)

335 and how epiphyte community structure varied between different forest types in the distant past.

336 A model system would also allow for rigorous testing of hypotheses on the evolution of

337 epiphytic leafy liverworts (Feldberg et al., 2014), lycophytes, and filicalean ferns (Lovis, 1977;

338 Schneider et al., 2004). Such a host organism would need to meet four requirements: (1) a

339 morphology that facilitates colonization by epiphytes; (2) morphological stasis over a wide

340 stratigraphic range; (3) widespread geographic distribution; and (4) abundance in the fossil

341 record.

342   Permineralized osmundaceous rhizomes satisfy these requirements for a model system to

343 track epiphyte community structure through time. (1) The leaf bases found at the periphery of

344 osmundaceous rhizomes have a rich microtopography that facilitates colonization by epiphytes.

345 Indeed, living osmundaceous fern rhizomes are often covered in epiphytes (Fig 3C). (2)

346 Osmundaceous ferns have been in morphological stasis since the Permian (> 250 million years)

347 (Miller, 1971; Bomfleur et al., 2017). (3) Osmundaceae were widespread geographically in the

348 geologic past (Miller, 1971; Bomfleur et al., 2017). (4) Osmundaceous ferns arguably have the

349 richest fossil record of any living fern lineage (Arnold, 1964; Miller, 1971; Tidwell and Ash,

350 1994; Bomfleur et al., 2017). Additionally, living osmundaceous ferns allow direct comparison

351 of the fossil epiphyte communities to their extant counterparts.

352   To date, permineralized osmundaceous rhizomes have yielded evidence for plant

353 interactions with invertebrates (Schopf, 1978; Tidwell & Clifford , 1995; Bomfleur, McLoughlin

354 & Vajda, 2014) and fungi (Kidston & Gwyne-Vaughan, 1907; Gould, 1970; Bomfleur,

355 McLoughlin & Vajda, 2014). These occurrences confirm that osmundaceous rhizomes were

356 important hosts for epiphyte communities in ancient ecosystems, just as they are today. Because

357 permineralized osmundaceous rhizomes represent a well-populated epiphyte niche that has

358 remained unchanged over time and space, and have a rich fossil record reaching into the

359 Permian, they provide a paleoecological model system for exploring epiphyte community

360 structure and evolution.

361

362 **Conclusions**

363   The complex community of organisms associated with an early Eocene osmundaceous

364 fern rhizome from Patagonia allows a glimpse of a tiny, ancient epiphyte community centered

365 around a single host plant. This community is surprisingly diverse and includes the first

366 fossilized leafy liverworts in South America, also marking the only fossil record of leafy

367 bryophyte epiphytes known outside of amber deposits; several types of fungal hyphae and

368 spores; microsclerotia with possible affinities in several ascomycete families; and oribatid

369 coprolites.

370   Understanding of complex epiphyte communities in fossil biotas, including detailed

371 insight into epiphyte communities like those of this Patagonian rhizome, is needed to paint a

372 more complete picture of life in the geologic past and to contextualize our understanding of

373 modern epiphyte communities. In the fossil record, complex epiphyte communities have only

374 been characterized in uncommon instances (e.g., the petrified forest of Chemnitz, Germany;

375 Rössler, 2000). In contrast to these rare occurrences, fossil osmundaceous ferns and the

376 communities they may harbor are widespread geographically and stratigraphically (Stewart &

377 Rothwell, 1993; Taylor, Taylor & Krings, 2009). Osmundaceous ferns can be traced back into

378 the Paleozoic (Miller, 1967, 1971; Stewart & Rothwell, 1993; Taylor, Taylor & Krings, 2009;

379 Bomfleur et al., 2017), a time when terrestrial ecological networks were becoming canalized

380 (DiMichele et al., 1992). Furthermore, osmundaceous morphology has been in stasis since the

381 Paleozoic (Eames, 1936; Stewart & Rothwell, 1993; Bomfleur et al., 2017). As such,

382 osmundaceous rhizomes represent a distinctive ecological niche, unchanged since the Permian,

383 and act as hosts for epiphyte communities comprised of plants, animals, and fungi. These

384 communities can also be studied in the modern biota and can be sampled systematically and

385 consistently across all occurrences, fossil and extant. Because of the scale of the organisms

386 (centimeter to decimeter), entire *in situ* tiny epiphyte communities can be studied directly in

387 fossil specimens. Thus, osmundaceous rhizomes represent an ecological niche that has remained

388 unchanged over time and provide a paleoecological model system for exploring epiphyte

389 community structure across geologic time and space. Given the diversity of epiphytes associated

390 with osmundaceous rhizomes from the La Huitrera Formation and the Jurassic of Sweden

391 (McLoughlin & Bomfleur, 2016), as well as the abundance of osmundaceous rhizomes in the

392 fossil record (Miller, 1967; Miller 1971; Taylor, Taylor & Krings, 2009; Bomfleur et al., 2017),

393 we predict that continued exploration will reveal additional aspects of the biotic networks

394 centered around these important repositories of ecological data from the geologic past.

395

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406

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Distribution of types of organisms colonizing the Patagonian osmundaceous rhizome (data point counts).

1 Table 1. Distribution of types of organisms colonizing the Patagonian osmundaceous rhizome
2 (data point counts).

Fern tissue type	Liverworts	Fungi in detritus	Coprolites	Gymnosperm root	Degraded cell content
Vascular tissue	0	1	8	0	2
Fiber ring	1	4	18	0	4
Parenchymatous mesophyll	1	77	26	0	1
External to fern tissue	20	88	7	1	0
Total	22	170	59	1	7

Figure 1

Component communities associated with an osmundaceous rhizome from the early Eocene of Patagonia.

(**A**) Composite image of cross section through the rhizome with vascular cylinder at center and numerous leaf traces in a helical pattern. The distribution of associated organisms is mapped in green (for leafy liverworts), light blue (fungi in detritus), purple (coprolites); arrowhead – gymnosperm root. Note denser colonization of the more degraded part of the rhizome at right. Scale bar = 1 cm.
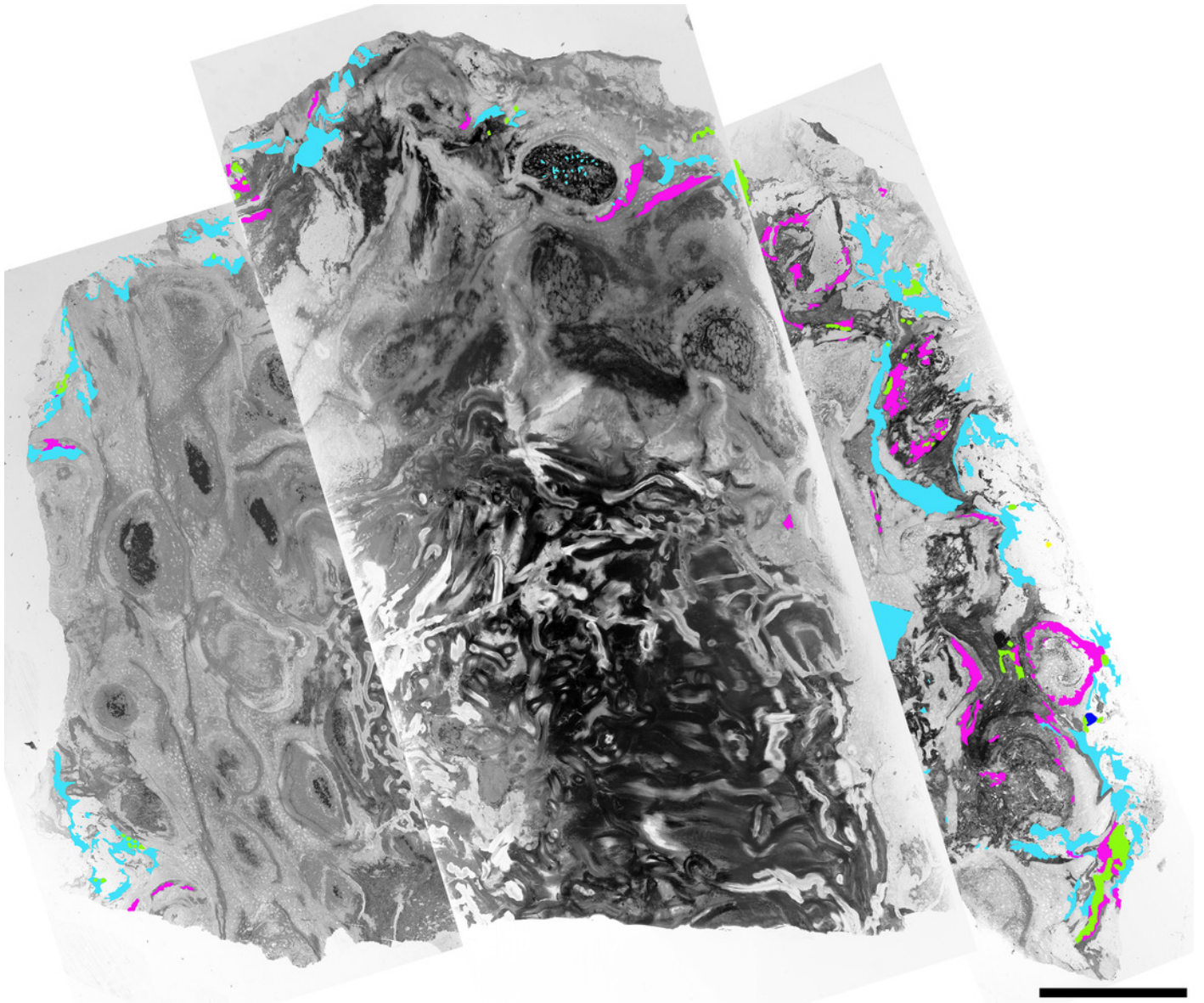
Figure 2

Diversity and distribution of organisms associated with the Patagonian rhizome.

(**A**) Longitudinal section of leafy liverwort gametophyte, showing two-ranked arrangement of ecostate leaves. (**B**) Cross sections of five branches of a leafy liverwort shoot. Note lack of lignified tissues in the stems and thin, ecostate leaves. (**C**) Oblique longitudinal section of a leafy liverwort stem (bottom) with two diverging branches. (**D**) Cross section of gymnosperm root with diarch protostele and secondary xylem. (**E**) Coprolite-filled gallery in osmundaceous leaf base. (**F**) Cerebriform microsclerotium in detritus around rhizome. (**G**) Three-celled stalked spores in detritus around rhizome (**H**) 7-8-celled stalked spores in detritus around rhizome. (**I**) Five-celled spores in detritus around rhizome. (**J**) Three-celled stalked spatulate spores in detritus around rhizome. (**K**) Three-celled stalked elliptical spores in detritus around rhizome. (**L**) Septate hyphae in detritus around the rhizome. (**M**) Circular structures of variable size filling a plant cell, thought to be the result of cell content degradation and aggregation during fossilization (**N**) Tissues of an osmundaceous leaf base diagrammed (**O**) Frequency of occurrence by tissue (same color coding as N) of each type of organismic remains associated with the Patagonian rhizome (right). See also Table 1. Scale bars: A-E 250 µm; F 25 µm; G-K, M 5 µm; L 2.5 µm
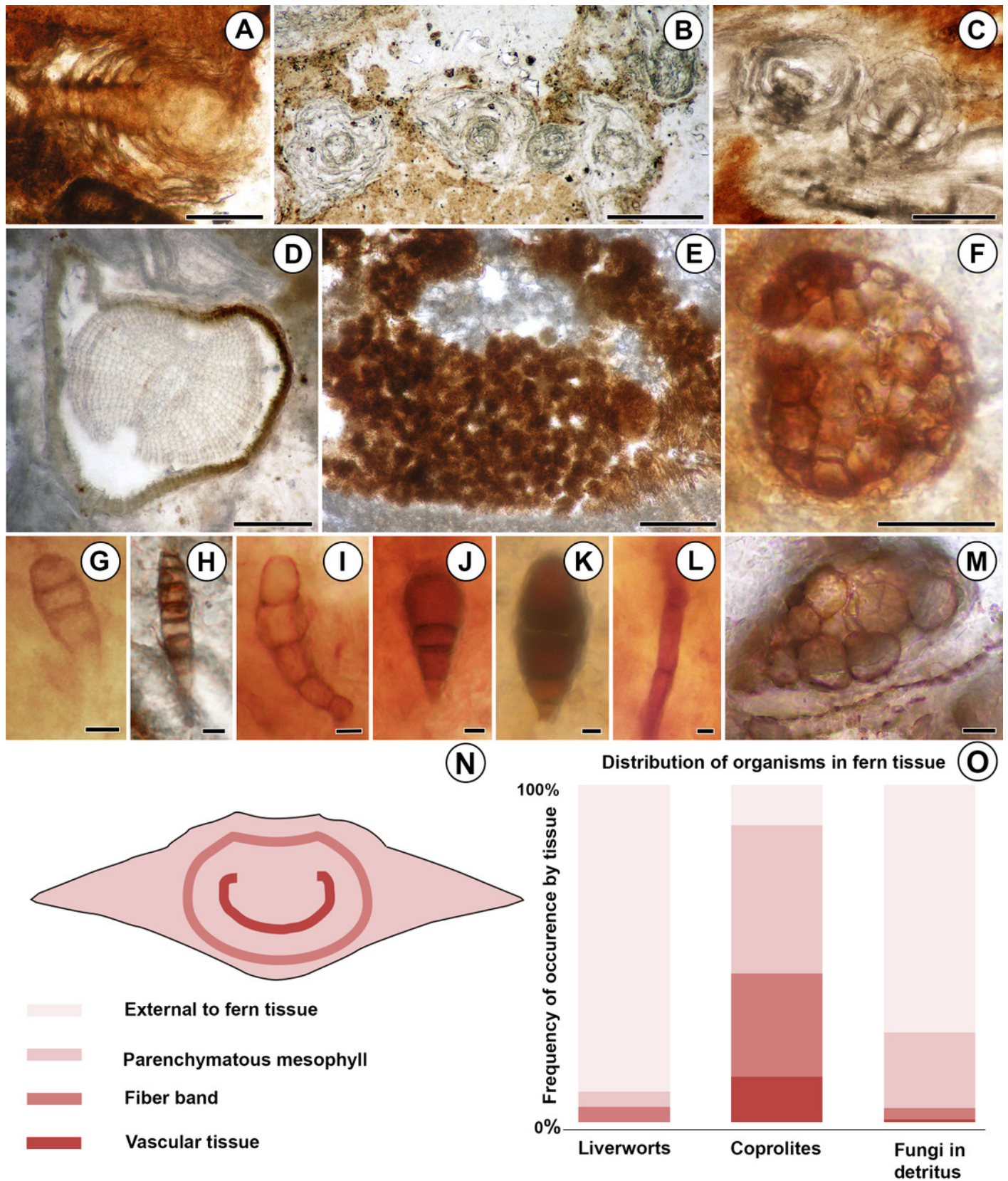
Figure 3

Preservation of Patagonian rhizome and densely colonized extant *Osmunda* L. rhizome.

(**A**) Partial cross section of the rhizome shown in Fig. 1 magnified to show gradient in preservation from periphery to center. (**B**) Cross section of a degraded leaf base with extensive coprolite-filled galleries. Coprolite-filled galleriesGalleries are highlighted in purple. (**C**) Extant *Osmunda regalis* L. rhizome in the Humboldt State University greenhouse showing abundant bryophyteepiphyte colonization. Scale bars: A 5 mm; B 1 mm.