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

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Background. In extant ecosystems, complex networks of ecological interactions between organisms can be readily studied. 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 plant-fossil record, despite their prominence in modern ecosystems. Accordingly, little is known about how terrestrial 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* (Osmundaceae) 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 and 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; as well as several types of fungal hyphae and spores; microsclerotia with possible affinities in several ascomycete families; and evidence for oribatid mites.

Discussion. The community associated with the Patagonian rhizome enriches our understanding of terrestrial 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 to explore 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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16

17 **Abstract**

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23 oviposition. Due to taphonomic biases, epiphyte communities are particularly rare in the plant-

24 fossil record, despite their prominence in modern ecosystems. Accordingly, little is known about

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30 Ma) Tufolitas Laguna del Hunco (Patagonia, Argentina) was studied in serial thin sections using

31 light microscopy. The community of organisms colonizing the tissues of the rhizome was

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39 record of leafy bryophyte epiphytes outside of amber deposits; as well as several types of fungal

40 hyphae and spores; microsclerotia with possible affinities in several ascomycete families; and

41 evidence for oribatid mites.

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43 The community associated with the Patagonian rhizome enriches our understanding of terrestrial

44 epiphyte communities in the distant past and adds to a growing body of literature on

45 osmundaceous rhizomes as important hosts for component communities in ancient ecosystems,

46 just as they are today. Because osmundaceous rhizomes represent an ecological niche that has

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49   structure through time.

50

Introduction

52   In the modern biota, direct access to living organisms has revealed significant portions of

53   their networks of ecological interactions. In contrast, understanding of such interactions is vastly

54   incomplete in ecosystems of the geologic past. Here, we investigate a complex community of

55   organisms that lived in association with an osmundaceous fern, preserved in Eocene rocks (ca.

56   52 Ma) of the Huitrera Formation, Argentinean Patagonia. The Huitrera Formation hosts one of

57   the most diverse Eocene floras characterized to date (Wilf et al., 2003, 2005a), yet the

58   interactions of plants in this flora with other organisms are just beginning to be characterized

59   (e.g., Wilf et al., 2005b). The fossil community associated with the osmundaceous fern is

60   surprisingly diverse and includes the first fossil epiphytic liverworts known outside of amber

61   deposits. Preserved in situ, this community offers a rare window onto aspects of ancient

62   ecosystems usually lost to time and taphonomic processes. Such ecologically relevant aspects of

63   community dynamics (abundance and diversity of epiphytes and incidence of herbivory),

64   typically unavailable for fossil associations, are described here. Rather than describing in detail

65   the biotic interactions between members of this community, here we aim to provide an

66   assessment of epiphyte community structure. We also use a broad definition of epiphyte, which

67   encompasses all organisms that live on a host plant (Steel and Bastow Wilson, 2003). Together,

68   the fossils represent a tiny epiphyte community centered around a single host plant.

69

Materials and Methods

71   <u>Geologic setting</u>

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

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

74   42°39'20.60", W 70°13'22.20". The source strata belong to the Tufolitas Laguna del Hunco, an

75   early Eocene, volcaniclastic, lacustrine caldera-fill deposit of the Huitrera Formation that is

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

77   1997). The new fossil site sits in the southern exposure area of the Tufolitas Laguna del Hunco,

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

79   1946; Wilf et al., 2003), which lies in the northeastern exposures of the same extensive, highly

80   fossiliferous unit. In this southern area, an ignimbrite that caps the fossil lake bed exposures ca.

81   5 km east of the new fossil site yielded an ^{40}Ar-^{39}Ar age on plagioclase of 49.26 ± 0.56 Ma (early

82   Eocene, Ypresian) in an unpublished thesis (Gosses, 2006; Gosses et al., 2006), directly

83   providing a minimum age for the osmundaceous rhizome. We note that this age has not been

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

85   be broadly accurate because it lies in correct stratigraphic order relative to other dated samples

86   from the Eocene caldera system (Gosses, 2006; Gosses et al., 2006; Tejedor et al., 2009).

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

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

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

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

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

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

93   Ypresian) following recalibration for modern decay constants (Wilf et al., 2003, 2005a, 2017;

94   Kuiper et al., 2008; Wilf, 2012). Thus, the osmundaceous rhizome can safely be considered

95   Ypresian and in the age range of ca. 49.3 to ca. 52.2 Ma. We prefer the older end of this range

96   because the dates from Laguna del Hunco, despite their ca. 24 km geographic distance from the

97   new fossil site, come from tuffs located within the Tufolitas Laguna del Hunco, the same unit

98   that holds the osmundaceous rhizome fossil. The dated ignimbrite in the southern area (Gosses,

99   2006; Gosses et al., 2006) lies above that unit.

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

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

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

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

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

105   2014).

106

107   <u>The host fern</u>

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

109   20 cm tall. This rhizome specimen and associated sterile foliage collected from the same locality

110   were recently described as *Todea* cf. *T. amissa* M. Carvalho (Bomfleur and Escapa, 2019), a

111   species initially described based on compressions of sterile and fertile foliage from the

112   northeastern exposures of Laguna del Hunco (Carvalho et al., 2013). The two records of *Todea*

113   in the Tufolitas Laguna del Hunco comprise the only South American fossil or extant record of

114   the genus (extant in Australia, New Guinea, and southern Africa; Carvalho et al., 2013).

115

116   <u>Methods</u>

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

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

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

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

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

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

123   Egidio Feruglio (MPEF-Pb), Trelew, Argentina, under catalog number MPEF-Pb 9299. The

124   distribution of colonizing organisms in fern tissue was quantified by superimposing a 200 μm x

125   200 μm grid onto the cross section of the rhizome (Fig. 1). At each intersection of the grid, we

126   recorded the type of fern tissue and the presence and types of colonizers. This process yielded

127   3,820 data points for the entire rhizome cross section. Of these, 252 data points included

128   colonizing organisms (see Table 1).

129

130   **Results**

131   <u>Epiphytic plants</u>

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

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

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

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

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

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

138   2A). Incompletely preserved, they are at least 490 μm long, lack a midrib, and are inserted at

139   30-40° angles (Fig. 2A-B). Their thickness (7.5-12.5 μm) indicates that they are probably

140   unistratose.

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

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

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

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

145

146 <u>Fungi</u>

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

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

149 2.0 µm in diameter; and (2) larger, septate hyphae 3.0-5.0 µm in diameter (Fig. 2L). The latter

150 have septae spaced at 21-22 µm; clamp connections were not observed.

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

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

153 42-50 µm in diameter and composed of isodiametric to oval cells 4-12 µm in size (Fig. 2F).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

169 is the most abundant fungal spore, three-celled, stalked and spatulate, ca. 25-30 µm long and 15

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

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

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

173 of slightly curved chains of five cells, ca. 38 µm long and 9 µm wide (Fig. 2I). The apical cell is

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

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

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

177

178 <u>Coprolites</u>

179 Small, spherical to ovoid coprolites occur towards the periphery of the rhizome, in

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

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

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

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

184

185 <u>Minute spherical structures</u>

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

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

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

189

190 **Discussion**

191 <u>Taxonomic affinities of epiphytes</u>

192

193 *Small epiphytic plants*

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

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

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

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

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

199 systematic placement of these plants.

200

201 *Root*

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

203   features typical of gymnosperms (Esau, 1965).

204

205   *Fungi*

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

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

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

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

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

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

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

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

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

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

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

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

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

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

220   2000); the extinct *C. eocenicum* Fritel et Viguier is especially similar to our type three spores,

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

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

223   inflated subapical cell (Elsik, 1993).

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

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

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

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

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

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

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

231   probably saprotrophs, rather than parasites or endophytes.

232

233   *Coprolites*

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

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

236   Bomfleur, 2016).

237

238   *Small spherical structures*

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

240   that the small, spherical structures are not microorganisms and are probably not of cellular

241   nature. Instead, they probably represent a type of cell content degradation and aggregation due

242   to the fossilization processes, also seen in the Early Devonian Rhynie chert plants (Michael

243   Krings, personal comm., 2017).

244

245   <u>Distribution patterns</u>

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

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

248   immediately prior to fossilization. Consistent with this interpretation, vascular tissues near the

249   center of the rhizome are well-preserved and are neither populated by colonizers (Fig. 1) nor

250   degraded (Figure 3A). However, some of the peripheral leaf bases are highly degraded,

251   surrounded by organic detritus (Figure 3A), and richly populated with colonizers (Fig. 1). The

252   leaf bases on one side of the rhizome are particularly degraded, and this region is most densely

253   colonized by epiphytic organisms (Fig. 1). Some leaf bases in this region contain coprolite-filled

254   galleries large enough to adversely affect the physiological functions and structural integrity of

255   these leaves (Figure 3B). Together, these observations indicate that the most degraded and

256   heavily colonized peripheral leaf bases were probably dead at the time of fossilization, whereas

257   the stem and more centrally-located, less degraded leaf bases were probably alive. This

258   distribution of degraded and living tissues is not surprising, since the rhizomes of living

259   Osmundaceae are often surrounded by a mantle of degraded and richly colonized dead leaf bases

260   (Fig. 3C).

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

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

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

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

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

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

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

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

269 arthropods that produced them did not have strong preferences for lignified or parenchymatous

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

271

272 <u>Comparison with the Jurassic community associated with *Osmundastrum pulchellum*</u>

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

274 associated with an exceptionally well preserved *Osmundastrum pulchellum* Bomfleur, G. Grimm

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

276 McLoughlin & Bomfleur, 2016; Bomfleur et al., 2017). Like the Patagonian community, this

277 Jurassic community included fungi, oribatid mites (coprolites) and epiphytic plants. However, in

278 the case of the *Osmundastrum pulchellum* community, the epiphytic plants are exclusively

279 vascular (lycopsids and ferns), which may indicate that bryophytes had not yet evolved the

280 epiphytic habit during the Jurassic. Additionally, fungal material is more abundant and diverse

281 in the Patagonian rhizome, probably correlated with higher proportions of decomposed tissues.

282 The richness of the communities associated with both of these osmundaceous rhizomes suggests

283 that other permineralized fern rhizomes are likely to yield diverse communities of associated

284 organisms.

285

286 <u>Significance of the leafy liverwort fossils</u>

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

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

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

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

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

292 et al., 2018). However, three additional compression fossils from the Carboniferous of Bolivia

293 and the Mesozoic of Argentina that lack cellular detail have also been compared with thalloid

294   liverworts (Jain and Delevoryas, 1967; Cardozo and Iannuzzi, 2004; Coturel and Savoretti,

295   2018).

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

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

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

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

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

301

302   Importance of understanding epiphyte communities in fossil biotas

303   Today, rich epiphyte communities are found on plants in several biomes, including boreal

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

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

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

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

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

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

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

311   Northwest North America, lichens and mosses may dominate (McCune, 1993), whereas

312   bromeliads and orchids may dominate epiphyte communities in a mid-elevation rainforest of

313   central Mexico (Hietz and Hietz-Seifert, 1995). The evolution of the deeply divergent epiphyte

314   communities in these biomes is critical for understanding the ecology and evolutionary history of

315   the forests themselves. However, our understanding of epiphyte community composition in the

316   distant past is poor and based on a small number of examples (e.g., Rothwell, 1991; Rössler,

317   2000; McLoughlin & Bomfleur, 2016).

318   Knowledge of complex epiphyte communities in fossil plant assemblages, including

319   detailed insight into component communities like those of the Patagonian rhizome, is needed to

320   paint a more complete picture of life in the geologic past and contextualize the evolution of

321   epiphyte communities. Past epiphyte communities probably provided the same kinds of

322   ecosystem services as those of the modern biota because these functions are independent of

323   epiphyte community structure. Thus, attempts to understand the ecology of these fossil biotas

324   without epiphytes ignore a critical component of the ecosystem. Similarly, an understanding of

325   ancient communities is required to place their modern counterparts in an evolutionary framework

326   (Gerhold et al., 2018).

327

328   <u>Osmundaceous rhizomes as a model system for understanding epiphyte community structure</u>

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

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

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

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

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

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

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

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

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

338   record.

339   Permineralized osmundaceous rhizomes satisfy these requirements. (1) The leaf bases

340   found at the periphery of osmundaceous rhizomes have a rich microtopography that facilitates

341   colonization by epiphytes. Indeed, living osmundaceous fern rhizomes are often covered in

342   epiphytes (Fig 3C). (2) Osmundaceous ferns have been in morphological stasis since the

343   Permian (> 250 million years; Miller, 1971; Bomfleur et al., 2017). (3) Osmundaceae were

344   widespread geographically in the geologic past (Miller, 1971; Bomfleur et al., 2017). (4)

345   Osmundaceous ferns arguably have the richest fossil record of any living fern lineage (Arnold,

346   1964; Miller, 1971; Tidwell and Ash, 1994; Bomfleur et al., 2017). Additionally, living

347   osmundaceous ferns allow direct comparison of the fossil epiphyte communities to their extant

348   counterparts.

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

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

351   Bomfleur, 2016) and fungi (Kidston & Gwyne-Vaughan, 1907; Gould, 1970; McLoughlin &

352   Bomfleur, 2016). These occurrences confirm that osmundaceous rhizomes were important hosts

353   for epiphyte communities in ancient ecosystems, just as they are today. Because permineralized

354   osmundaceous rhizomes represent a well-populated epiphyte niche that has remained unchanged

355   over time and space and have a rich fossil record reaching into the Permian, they provide a

356   paleoecological model system for exploring epiphyte community structure and evolution.

357

358   **Conclusions**

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

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

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

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

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

364   spores; microsclerotia with possible affinities in several ascomycete families; and coprolites

365   produced by oribatid mites.

366   Understanding of complex epiphyte communities in fossil plant assemblages is needed to

367   accurately understand ecological networks within extinct ecosystems and to unearth the

368   evolutionary history of extant epiphytes. In the fossil record, complex epiphyte communities on

369   plants have only been characterized in uncommon instances (e.g., the petrified forest of

370   Chemnitz, Germany; Rössler, 2000). In contrast to these rare occurrences, fossil osmundaceous

371   ferns and the communities they may harbor are widespread geographically and stratigraphically

372   (Stewart & Rothwell, 1993; Taylor, Taylor & Krings, 2009). Osmundaceous ferns can be traced

373   back into the Paleozoic (Miller, 1967, 1971; Stewart & Rothwell, 1993; Taylor, Taylor &

374   Krings, 2009; Bomfleur et al., 2017), a time when terrestrial ecological networks were becoming

375   canalized (DiMichele et al., 1992). Furthermore, osmundaceous morphology has been in stasis

376   since the Paleozoic (Eames, 1936; Stewart & Rothwell, 1993; Bomfleur, McLoughlin & Vajda,

377   2014). As such, osmundaceous rhizomes represent a distinctive ecological niche, unchanged

378   since the Permian, and act as hosts for epiphyte communities comprised of plants, animals, and

379   fungi. These communities can also be studied in the modern biota and can be sampled

380   systematically and consistently across all occurrences, fossil and extant. Because of the scale of

381   the organisms (centimeter to decimeter), entire *in situ* tiny epiphyte communities can be studied

382   directly in fossil specimens. Thus, osmundaceous rhizomes represent an ecological niche that

383   has remained unchanged over time and provide a paleoecological model system for exploring

384   epiphyte community structure across geologic time and space. Given the diversity of epiphytes

385   associated with osmundaceous rhizomes from the Huitrera Formation and the Jurassic of Sweden

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

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

388   predict that continued exploration will reveal additional aspects of the biotic networks centered

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

390

403

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574

Table 1(on next page)

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).

3

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

4

Figure 1

Component communities associated with a *Todea* rhizome from the early Eocene of Patagonia, specimen MPEF-Pb 9299.

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.
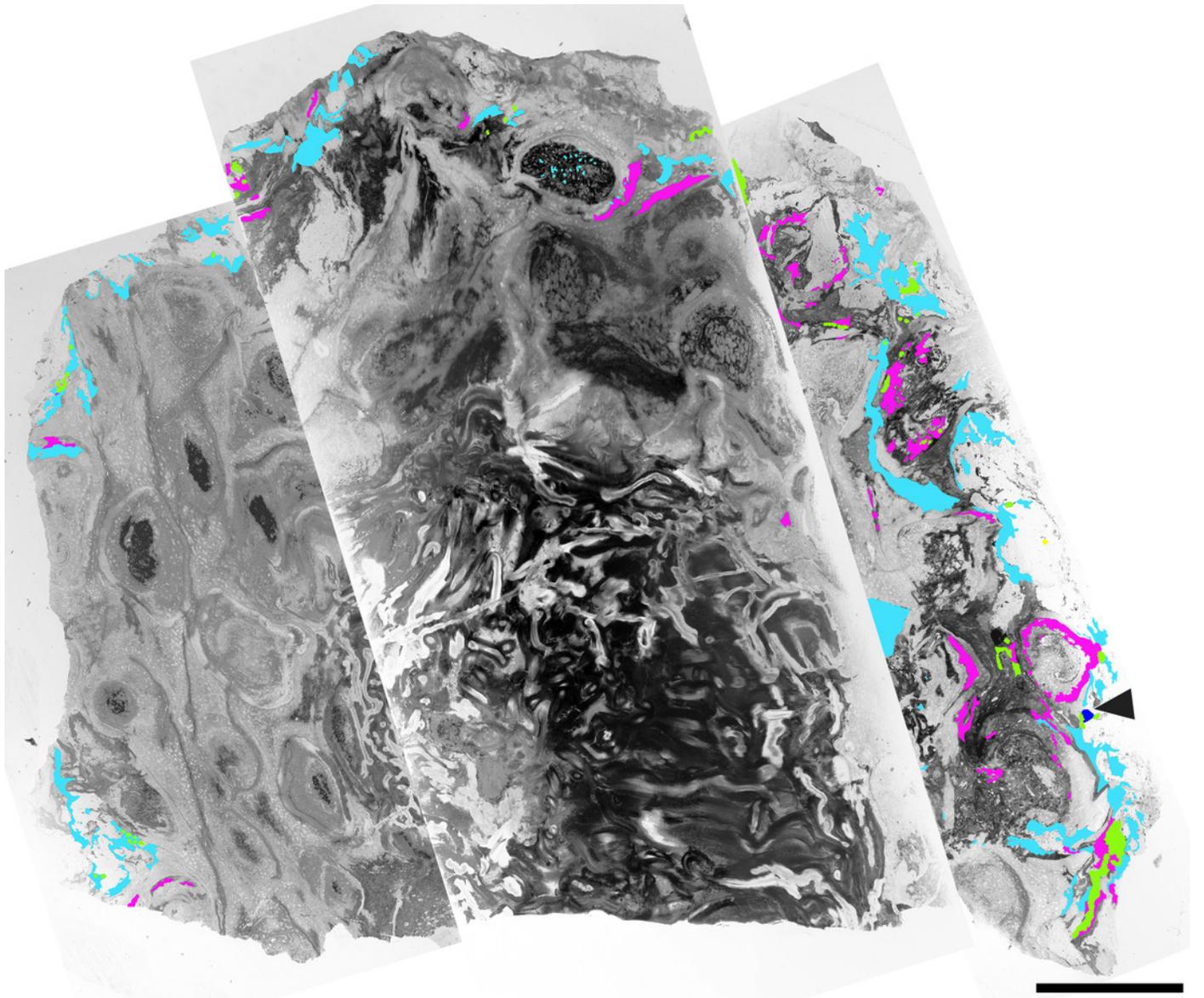
Figure 2

Figure 2. Diversity and distribution of organisms associated with the Patagonian *Todea* 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**) Seven to eight-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. See also Table 1. Scale bars: A-E 250 μm; F 25 μm; G-K, M 5 μm; L 2.5 μm.
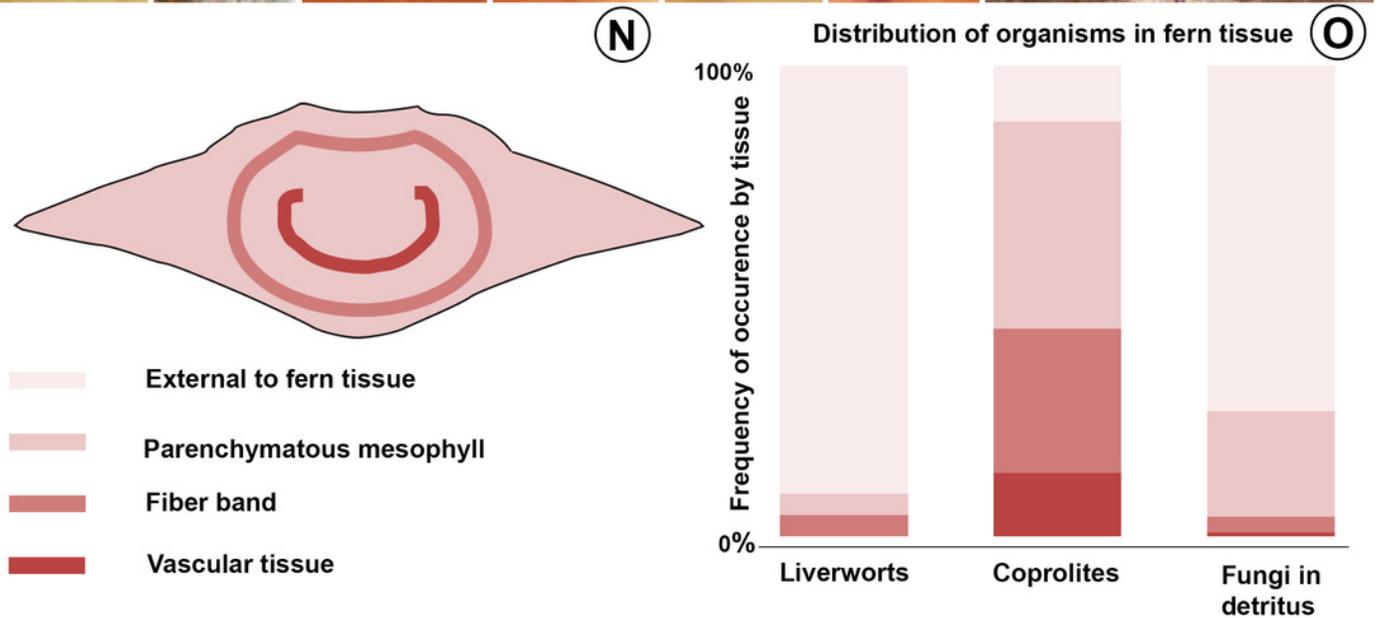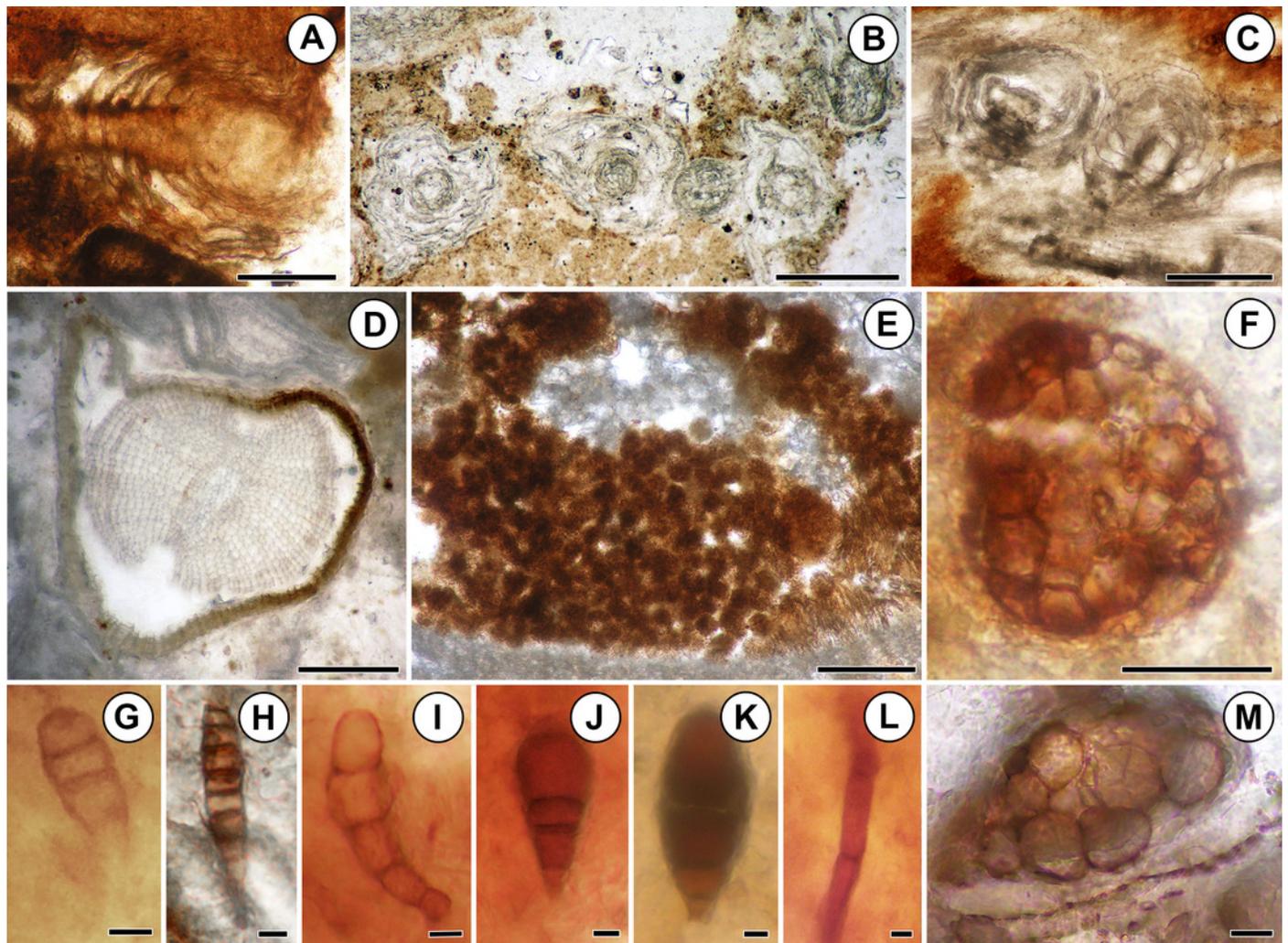
Figure 3

Preservation of the Patagonian *Todea* 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 galleries are highlighted in purple. (**C**) Extant*Osmunda regalis*L. rhizome in the Humboldt State University greenhouse showing abundant epiphyte colonization. Scale bars: A 5 mm; B 1 mm.