Fossil fern rhizomes as a model system for biotic interactions 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 that form these networks. In contrast, understanding of such interactions in ecosystems of the geologic past is incomplete. Specifically, in terrestrial ecosystems we know comparatively little about plant biotic interactions besides herbivory, oviposition, galling. Here we describe a tiny in situ fossil community which sheds light on concurrent plant-plant, plant-fungal, and plant-animal interactions.

Methods. A single silicified osmundaceous rhizome from a new locality of the early Eocene (ca. 52 Ma) Tufolitas Laguna del Hunco 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. For this, 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; several types of fungal hyphae and spores; microsclerotia with probable affinities in several ascomycete families; and oribatid mite coprolites.

Discussion. The community associated with the Patagonian rhizome enriches our understanding of plant biotic interactions in the distant past and adds to a growing body of literature, which indicates that osmundaceous rhizomes were important hosts for component communities in ancient ecosystems, just as they are today. Because osmundaceous rhizomes represent an ecological niche that has remained unchanged over time and space, and are abundant in the fossil record, they provide a good paleoecological model system that could be used for exploring plant biotic interactions across geologic time.

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13

14 **Abstract**

15 **Background.**

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17 readily obtained, due to the ease of unlimited access to the living organisms that form these

18 networks. In contrast, understanding of such interactions in ecosystems of the geologic past is

19 incomplete. Specifically, in terrestrial ecosystems we know comparatively little about plant

20 biotic interactions besides herbivory, oviposition, galling. Here we describe a tiny in situ fossil

21 community which sheds light on concurrent plant-plant, plant-fungal, and plant-animal

22 interactions.

23 **Methods.**

24 A single silicified osmundaceous rhizome from a new locality of the early Eocene (ca. 52 Ma)

25 Tufolitas Laguna del Hunco was studied in serial thin sections using light microscopy. The

26 community of organisms colonizing the tissues of the rhizome was characterized by identifying

27 the organisms, as well as mapping and quantifying their distribution. For this, a 200 x 200 µm

28 grid was superimposed onto the rhizome cross section and the colonizers present at each node of

29 the grid were tallied.

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

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

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

34 record of leafy bryophyte epiphytes; several types of fungal hyphae and spores; microsclerotia

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37 The community associated with the Patagonian rhizome enriches our understanding of plant

38 biotic interactions in the distant past and adds to a growing body of literature, which indicates

39 that osmundaceous rhizomes were important hosts for component communities in ancient

40 ecosystems, just as they are today. Because osmundaceous rhizomes represent an ecological

41 niche that has remained unchanged over time and space, and are abundant in the fossil record,

42 they provide a good paleoecological model system that could be used for exploring plant biotic

43 interactions across geologic time.

44

Introduction

45

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

47 network of ecological interactions. In contrast, understanding of such interactions is incomplete

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

49 comparatively little about plant biotic interactions besides herbivory, oviposition, galling

50 (DiMichele et al., 1992; Labandiera & Currano, 2013). Here, we investigate a complex

51 community of organisms that lived in association with an osmundaceous fern, preserved in

52 Eocene rocks (ca. 52 Ma) of La Huitrera Formation, Argentinean Patagonia. La Huitrera

53 Formation hosts one of the most diverse Eocene floras characterized to date (Wilf et al., 2003;

54 Wilf et al., 2005a) yet the interactions of plants in this flora with other organisms are just

55 beginning to be characterized (Wilf et al., 2005b). The fossil community associated with the

56 osmundaceous fern is surprisingly diverse and includes the first fossil epiphytic liverworts.

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

58 usually lost to time and taphonomic processes. Such ecologically relevant aspects of *concurrent*

59 plant-plant, plant-fungus, and animal-plant interactions (abundance and diversity of epiphytes

60 and fungal decomposers, incidence of herbivory), typically unavailable for fossil associations,

61 are described here. Together, these fossils represent a tiny ecosystem centered around a single

62 host plant. Osmundaceous ferns have been recognized in rocks as old as the Permian and their

63 morphology has been in stasis ever since (Eames, 1936; Stewart & Rothwell, 1993; Taylor,

64 Taylor & Krings, 2009). Consequently, osmundaceous rhizomes represent an ecological niche

65 that has changed little over time and space, thus providing a paleoecological model system for

66 exploring plant biotic interactions across geologic time.

67

Materials and Methods

68

69 <u>Geologic setting</u>

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

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

72 42°39'20.60", W 70°13'22.20". The source strata belong to the Tufolitas Laguna del Hunco, an

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

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

75 1997) The new fossil site sits in the southern exposure area of the Tufolitas Laguna del Hunco,

76   ca. 24 km SSW of the well-known Laguna del Hunco fossil locality (Berry, 1925; Wilf et al.,

77   2003; Petersen, 1946), which lies in the northeastern exposures of the same extensive, highly

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

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

80   2009). In this southern area, an ignimbrite that caps the fossil lake bed exposures ca. 5 km east

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

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

83   minimum age for the "tiny ecosystem" fossils. We note that this age has not been subsequently

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

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

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

87   2009). 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; Wilf et al., 2005). The most reliable radiometric age at

91   Laguna del 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; Wilf et al.,

94   2005; Kuiper et al., 2008; Wilf, 2012; Wilf et al., 2017). Thus, the "tiny ecosystem" can safely

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

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

97   distance from the new fossil site, come from tuffs located within the Tufolitas Laguna del

98   Hunco, the same unit that holds the "tiny ecosystem" fossils. The dated ignimbrite in the

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

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

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

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

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

104   fossils of *Agathis* (Araucariaceae) and *Eucalyptus* (Myrtaceae) (Wilf et al., 2013; Gondalfo et al.,

105   2011; Wilf et al., 2014). Of significance here, the Gondwanic character of the flora also extends

106   to the ferns, which include compressed fertile and sterile foliage of *Todea amissa*

107 (Osmundaceae) that comprise the only South American fossil or extant record of *Todea* (extant

108 in Australia, New Guinea, and southern Africa) (Carvahlo et al., 2013).

109 Methods

110   The osmundaceous rhizome, preserved by silicification, has been studied in serial thin

111 sections using light microscopy. Photographs of whole thin sections were taken using a light box

112 and a Canon EOS 70D Camera fitted with a Canon 60mm macro lens, and stitched together

113 using Photoshop CC (Adobe, San Jose, California, USA). All other micrographs were taken

114 using a Nikon Coolpix E8800 digital camera mounted on a Nikon Eclipse E400 microscope and

115 processed using Photoshop CC. All specimens and preparations are housed in the collections of

116 the Museo Paleontologico Egidio Feruglio (MPEF), Trelew, Argentina. The distribution of

117 colonizing organisms in fern tissue was measured by superimposing a 200 μm x 200 μm grid

118 onto the cross section of the rhizome (Fig. 1a). At each intersection of the grid, we recorded the

119 type of fern tissue and the presence and type of colonizers. This yielded 3820 data points for the

120 entire rhizome cross section. Of these, 252 data points included colonizing organisms (see Table

121 1).

122 **Results**

123 The host fern

124   The single anatomically-preserved osmundaceous rhizome (MPEF-Pb 9299) was

125 collected from a newly discovered early Eocene locality of the Tufolitas Laguna del Hunco, La

126 Huitrera Formation (see geologic setting for details), Argentine Patagonia (NW Chubut

127 Province). At other sites, this formation has yielded a diverse compression flora that includes

128 fertile osmundaceous foliage (*Todea amissa* M. Carvalho – see geologic setting for details). The

129 rhizome, a fragment ca. 20 cm tall x 7.5 cm in diameter, shows all the features typical of

130 osmundaceous fern stems: upright habit, characteristic dictyostele and dense persistent leaf bases

131 with adaxially concave xylem strands, sclerenchymatous rings, and rhomboidal parenchymatous

132 wings (Eames, 1936). The biota hosted by this rhizome includes epiphytic bryophytes, diverse

133 fungi, and arthropods (coprolites).

134

135 Rhizome epiphytes

136   More than 100 small leafy shoots are found, primarily along the outer perimeter of one

137 side of the rhizome, but also between leaf bases elsewhere along the rhizome (Fig. 1a). These

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

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

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

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

142   2a). Incompletely preserved, they are at least 490 μm long, lack a midrib, and are inserted at 30-

143   40° angles (Fig. 2a). Their thickness (7.5-12.5 μm) indicates that they are probably unistratose.

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

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

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

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

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

149   systematic placement of these plants.

150   In addition, a small root was found in the detritus at the periphery of the rhizome (Fig.

151   1a). The root is 0.7 mm in diameter and has a diarch protostele ca. 100 μm wide (Fig. 2d).

152   Secondary xylem with narrow (10-21 μm) tracheids (Fig. 2d) comprises ca. 75 % of the root;

153   some bark is also preserved (Fig. 2d). The diarch primary xylem and high proportion of

154   secondary xylem lacking vessels are features typical of gymnosperms (Esau, 1965).

155

156   Fungi

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

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

159   2.0 μm in diameter; and (2) larger, septate hyphae 3.0-5.0 μm in diameter (Fig. 2l). The latter

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

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

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

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

164   These microsclerotia are similar in size and morphology to cerebriform microsclerotia described

165   in the roots of *Eorhiza arnoldii* Robison et Person from the Eocene of Canada, which were

166   attributed to dark septate endophytes, a lineage of dematiaceous ascomycetes (Klymiuk, Taylor

167   & Taylor, 2013b).

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

169   associated with the rhizome (Fig. 1a, 2g-k). These reproductive structures are multicellular

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

171   of the five types are preserved with narrow stalks (Fig. 2g, 2h-k). A first type consists of stalked,

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

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

174   >10 µm long and 6 µm wide, tapering basally into a stalk 4 µm wide. Type two includes three

175   celled, stalked spores roughly elliptical in shape, ca. 40 µm long and up to 16 µm wide (Fig. 2k).

176   The apical cell is shaped like a truncated ellipse, 18 µm long and 16 µm wide. The subapical

177   cell is rectangular, 11 µm long x 16 µm wide. The basal cell is trapezoidal, 6 µm long and 13

178   µm wide apically, tapering to 6 µm basally. The stalk tapers to 4 µm. Type three consists of

179   elongate, stalked, 7- or 8-celled spores ca. 35 µm long and 6 µm wide (Fig. 2h). Cells, except

180   for the basal and apical ones, are rectangular, 3-5 µm long x 6 µm wide. The apical cell is

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

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

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

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

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

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

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

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

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

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

191   In terms of potential taxonomic affinities, type one spores compare in overall

192   morphology to smaller members of the dispersed fossil spore genus *Diporicellaesporites* Elsik,

193   especially *D. minisculus* Sheffy et Dilcher, but the pores diagnostic of this genus (Kalgutkar &

194   Jansonius, 2000) are not observable in the Argentinean material. Type two and four spores are

195   comparable to species of the dispersed spore genus *Brachysporites* Lange et Smith, whose

196   multicellular, usually spatulate spores resemble conidia of the extant dematiaceous ascomycete

197   genus *Brachysporium* Saccardo (Kalgutkar & Jansonius, 2000; Taylor, Krings & Taylor, 2015).

198   Within *Brachysporites*, type two spores are most similar to *B. atratus* Kalgutkar, while type four

199   spores are most similar to *B. pyriformis* Lange et Smith (Kalgutkar & Jansonius, 2000). Type

200   three spores are comparable to conidia of the extant magnaporthaceous ascomycete

201   *Clasterosporium* Schwein. (Kalgutkar & Jansonius, 2000); the extinct *C. eocenicum* Fritel et

202   Viguier is especially similar to type three spores, although the latter are slightly smaller. Type

203   five spores are comparable to the conidia of the extant pleosporaceous ascomycete *Curvularia*

204   Boedijn based on their size, curved shape, and inflated subapical cell (Elsik, 1993).

205   Overall, the fungal reproductive structures documented on the Patagonian rhizome are

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

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

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

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

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

211   material (Fig. 1a), these fungi were probably saprotrophs, rather than parasites or endophytes.

212

213   <u>Coprolites</u>

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

215   excavations of the parenchymatous mesophyll, fiber band, and vascular tissue (Fig. 1a, 2e).

216   Coprolites also occur externally to fern tissues, in highly degraded portions of the rhizome (Fig.

217   1a). They have smooth surfaces and are 23-260 µm in diameter, composed of angular cell-wall

218   fragments and opaque bodies (Fig. 2e). Based on their size, shape and texture, the excavations

219   and coprolites were probably produced by oribatid mites (Labandiera, 1998; Kellogg & Taylor,

220   2004; McLoughlin and Bomfleur, 2016).

221

222   <u>Degraded cell contents</u>

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

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

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

226   perfectly circular shape, tendency to completely fill cells, and variable size indicate that these

227   structures are not microorganisms. Instead, they probably represent a particular type of cell

228   content degradation and aggregation due to the fossilization processes, also seen in the Early

229   Devonian Rhynie chert plants (Michael Krings, personal comm., 2017).

230

231   **Discussion**

232   Distribution patterns

233   It is unclear whether this fern rhizome was living at the time of permineralization.

234   Nevertheless, a variety of biotic interactions, involving arthropods, liverworts, fungi and vascular

235   plants, were clearly occurring, covering the rhizome in several kinds of life (Fig. 1a) just like

236   extant osmundaceous rhizomes (Fig. 1b). The distribution and frequency of each kind of

237   organism associated with the rhizome by tissue type (Fig. 2n; Table 1) show that most associated

238   organisms are much more abundant in the more degraded region of the rhizome (Fig. 1a).

239   Liverworts and fungi in detritus are found primarily external to the fern tissues, and secondarily

240   in some of the most degraded tissues near the periphery of the rhizome (Fig. 1a, 2n). Coprolites

241   also occur in all types of tissue, as well as externally to some of the most degraded leaf bases,

242   indicating that the arthropods that produced them did not have strong preference for lignified or

243   parenchymatous tissues (Fig. 1a, 2n).

244

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

246   A similar community of organisms has been described associated with an exceptionally

247   well preserved *Osmunda pulchella* Bomfleur, G. Grimm et McLoughlin rhizome from the

248   Jurassic of Sweden (Bomfleur, McLoughlin & Vajda, 2014; McLoughlin & Bomfleur, 2016).

249   Like the Patagonian rhizome, this Jurassic community included fungi, oribatid mites (coprolites)

250   and epiphytes. However, in the case of the *Osmunda pulchella* community, the epiphytes are

251   exclusively vascular (lycopsid roots, fern leptosporangia, spores). Additionally, fungal material

252   is more abundant and diverse in the Patagonian rhizome, probably correlated with higher

253   proportions of decomposed tissues. The richness of both these communities associated with

254   osmundaceous rhizomes suggests that other permineralized fern rhizomes may also host diverse

255   associations of organisms and serve as models for understanding biotic interactions in deep time.

256

257   Significance of the leafy liverwort fossils

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

259   Tomescu, A. M. F. unpublished data), it is not surprising that these tiny epiphytes represent the

260   first report of fossil leafy liverworts from South America. *Marchantites hallei* Lundblad

261   (Lundblad, 1955), a thalloid liverwort from the Early Cretaceous of Argentina, is the only other

262   unequivocal fossil liverwort known from South America (Oostendorp, 1987; Tomescu, A. M. F.

263   unpublished data). Additionally, the liverworts described here are the first epiphytic leafy

264   gametophytes in the fossil record. All other fossils of epiphytic bryophytes are moss

265   protonemata described on angiosperm leaves (Mägdefrau, 1956; Selkirk, 1974; Barclay et al.,

266   2013).

267

268   **Conclusions**

269   The complex community of organisms associated with the Patagonian osmundaceous

270   fern rhizome allows a glimpse of a tiny, ancient ecosystem centered around a single host plant.

271   This community is surprisingly diverse and includes the first fossilized leafy liverworts in South

272   America, also marking the only fossil record of leafy bryophyte epiphytes; several types of

273   fungal hyphae and spores; microsclerotia with probable affinities in several ascomycete families;

274   and oribatid coprolites. Understanding of complex interactions in fossil biotas, including

275   detailed insight into component communities like those of this Patagonian rhizome, is needed to

276   paint a more complete picture of life in the geologic past. In the fossil record, complex

277   interactions of plants have only been characterized in uncommon instances (e.g., Rhynie chert,

278   the petrified forest of Chemnitz; Rössler, 2000; Taylor et al., 2004). In contrast to these rare

279   occurrences, fossil osmundaceous ferns and the communities they may harbor are widespread

280   geographically and stratigraphically(Stewart & Rothwell, 1993; Taylor, Taylor & Krings, 2009).

281   Osmundaceous ferns can be traced back into the Paleozoic (Miller, 1967; Miller, 1971; Stewart

282   & Rothwell, 1993; Taylor, Taylor & Krings, 2009) at a time when ecological networks were

283   becoming canalized (DiMichele et al., 1992). Furthermore, osmundaceous morphology has been

284   in stasis since the Paleozoic (Eames, 1936; Stewart & Rothwell, 1993). As such, osmundaceous

285   rhizomes represent a distinctive ecological niche, unchanged since the Permian, and acts as a hub

286   for interactions between plants, fungi, and animals, which can also be studied in the modern

287   biota and can be sampled systematically and consistently across all occurrences, fossil and

288   extant. Because of the scale of these interactions (centimeter to millimeter), entire in situ tiny

289   ecosystems and the interactions within can be studied directly in fossil specimens. To date,

290   permineralized osmundaceous rhizomes have yielded evidence for plant interactions with

291   invertebrates (Schopf, 1978; Tidwell & Clifford , 1995; Bomfleur, McLoughlin & Vajda, 2014)

292   and fungi (Kidston & Gwyne-Vaughan, 1907; Gould, 1970; Bomfleur, McLoughlin & Vajda,

293   2014). These occurrences confirm that osmundaceous rhizomes were important hosts for

294   component communities in ancient ecosystems, just as they are today. Because osmundaceous

295   rhizomes represent an ecological niche that has remained unchanged over time and space, they

296   provide a paleoecological model system for exploring plant biotic interactions across geologic

297   time. Given the diversity of interactions recently recorded in La Huitrera Formation and the

298   Jurassic of Sweden, as well as the abundance of osmundaceous rhizomes in the fossil record

299   (Miller, 1967; Miller 1971; Taylor, Taylor & Krings, 2009), we predict that continued

300   exploration will reveal additional aspects of the biotic networks centered around these important

301   repositories of ecological data from the geologic past.

302

303   **Acknowledgements**

310

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Table 1(on next page)

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

Table 1. Distribution of types of organisms colonizing the Patagonian osmundaceous rhizome (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. (**b**) Extant *Osmunda regalis* L. rhizome showing abundant bryophyte colonization.
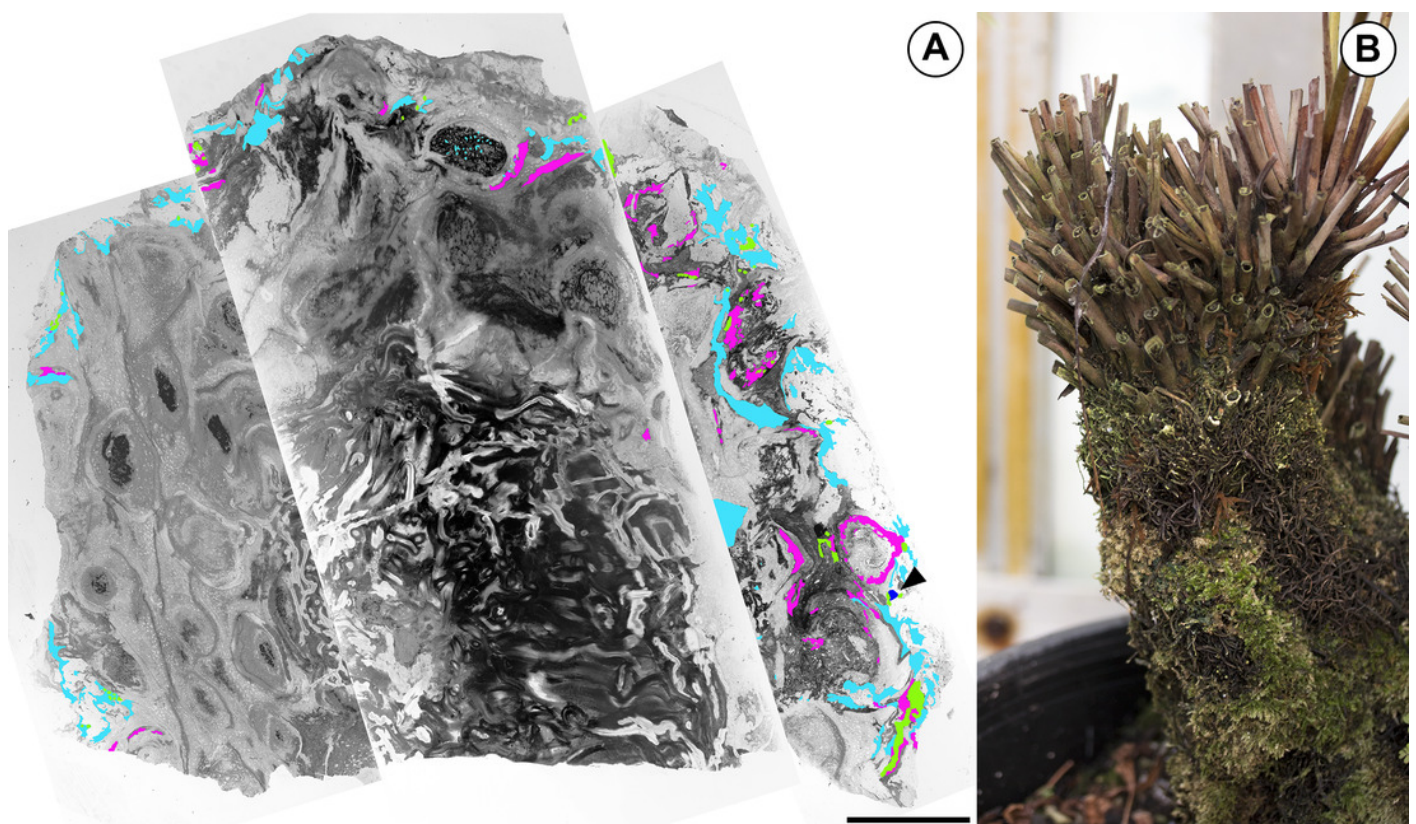
Figure 2

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 (left) and frequency of occurrence by tissue (same color coding) of each type of organismic remains associated with the Patagonian rhizome (right). See also Table S1. Scale bars: a-e 250 μm; f 25 μm; g-k, m 5 μm; l 2.5 μm.