

# Fossil fern rhizomes as a model system for biotic interactions across geologic time: Evidence from Patagonia (#21919)

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# 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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# **Abstract**

## **Background.**

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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.

# Introduction

In the modern biota, direct access to organisms has revealed significant parts of their network of ecological interactions. In contrast, understanding of such interactions is incomplete in ecosystems of the geologic past. Specifically, in terrestrial ecosystems we know comparatively little about plant biotic interactions besides herbivory, oviposition, galling (DiMichele et al., 1992; Labandiera & Currano, 2013). Here, we investigate a complex community of organisms that lived in association with an osmundaceous fern, preserved in Eocene rocks (ca. 52 Ma) of La Huitrera Formation, Argentinean Patagonia. La Huitrera Formation hosts one of the most diverse Eocene floras characterized to date (Wilf et al., 2003; Wilf et al., 2005a) yet the interactions of plants in this flora with other organisms are just beginning to be characterized (Wilf et al., 2005b). The fossil community associated with the osmundaceous fern is surprisingly diverse and includes the first fossil epiphytic liverworts. Preserved in situ, this community offers a rare window onto aspects of ancient ecosystems usually lost to time and taphonomic processes. Such ecologically relevant aspects of *concurrent* plant-plant, plant-fungus, and animal-plant interactions (abundance and diversity of epiphytes and fungal decomposers, incidence of herbivory), typically unavailable for fossil associations, are described here. Together, these fossils represent a tiny ecosystem centered around a single host plant. Osmundaceous ferns have been recognized in rocks as old as the Permian and their morphology has been in stasis ever since (Eames, 1936; Stewart & Rothwell, 1993; Taylor, Taylor & Krings, 2009). Consequently, osmundaceous rhizomes represent an ecological niche that has changed little over time and space, thus providing a paleoecological model system for exploring plant biotic interactions across geologic time.

# Materials and Methods

## Geologic setting

The fossils described here come from a new site ca. 2.1 km south of the Chubut River and 9.8 km due west of Piedra Parada in northwestern Chubut Province, Patagonian Argentina, S 42°39'20.60", W 70°13'22.20". The source strata belong to the Tufolitas Laguna del Hunco, an early Eocene, volcanoclastic, caldera-fill lacustrine deposit of La Huitrera Formation that is embedded in the Middle Chubut River Volcanic-Pyroclastic Complex (Aragón and Mazzoni, 1997) The new fossil site sits in the southern exposure area of the Tufolitas Laguna del Hunco,

ca. 24 km SSW of the well-known Laguna del Hunco fossil locality (Berry, 1925; Wilf et al., 2003; Petersen, 1946), which lies in the northeastern exposures of the same extensive, highly fossiliferous unit. This is the first report of fossil plants from the southern exposures, although the nearby Laguna Fría mammal assemblage potentially correlates to these strata (Tejedor et al., 2009). In this southern area, an ignimbrite that caps the fossil lake bed exposures ca. 5 km east of the new fossil site yielded an  $^{40}\text{Ar}$ - $^{39}\text{Ar}$  age on plagioclase of  $49.26 \pm 0.56$  Ma (early Eocene, Ypresian) in an unpublished thesis (Gosses, 2006; Gosses et al., 2006), directly providing a minimum age for the “tiny ecosystem” fossils. We note that this age has not been subsequently vetted or revised for updated decay constants (Kuiper et al., 2008), but it is likely to be broadly accurate because it lies in correct stratigraphic order relative to other dated samples from the Eocene caldera system (Gosses, 2006; Gosses et al., 2006; Kuiper et al., 2008; Tejedor et al., 2009). At Laguna del Hunco (northeastern exposures), three  $^{40}\text{Ar}$ - $^{39}\text{Ar}$  ages from volcanic ashes and two recorded paleomagnetic reversals, all from strata located within the main fossiliferous section of the Tufolitas Laguna del Hunco, constrain the time of fossil deposition there to the early Eocene as well (Wilf et al., 2003; Wilf et al., 2005). The most reliable radiometric age at Laguna del Hunco, on sanidines from an ash taken from the middle of the most densely sampled fossiliferous interval and analyzed in two different labs, is  $52.22 \pm 0.22$  Ma (early Eocene, Ypresian) following recalibration for modern decay constants (Wilf et al., 2003; Wilf et al., 2005; Kuiper et al., 2008; Wilf, 2012; Wilf et al., 2017). Thus, the “tiny ecosystem” can safely be considered Ypresian and in the age range of ca. 49.3 to perhaps 52.5 Ma. We prefer the older end of this range because the dates from Laguna del Hunco, despite their ca. 24 km geographic distance from the new fossil site, come from tuffs located within the Tufolitas Laguna del Hunco, the same unit that holds the “tiny ecosystem” fossils. The dated ignimbrite in the southern area (Gosses, 2006; Gosses et al., 2006) lies above that unit.

At Laguna del Hunco itself, the Tufolitas Laguna del Hunco hosts one of the most diverse Eocene compression floras known (Wilf et al., 2003; Wilf et al., 2005). The flora has a robust Gondwanic component displayed among its gymnosperm and angiosperm species, as described extensively elsewhere; among the most striking occurrences are the well-preserved and abundant fossils of *Agathis* (Araucariaceae) and *Eucalyptus* (Myrtaceae) (Wilf et al., 2013; Gondolfo et al., 2011; Wilf et al., 2014). Of significance here, the Gondwanic character of the flora also extends to the ferns, which include compressed fertile and sterile foliage of *Todea amissa*



(Osmundaceae) that comprise the only South American fossil or extant record of *Todea* (extant in Australia, New Guinea, and southern Africa) (Carvalho et al., 2013).

# Methods

The osmundaceous rhizome, preserved by silicification, has been studied in serial thin sections using light microscopy. Photographs of whole thin sections were taken using a light box and a Canon EOS 70D Camera fitted with a Canon 60mm macro lens, and stitched together using Photoshop CC (Adobe, San Jose, California, USA). All other micrographs were taken using a Nikon Coolpix E8800 digital camera mounted on a Nikon Eclipse E400 microscope and processed using Photoshop CC. All specimens and preparations are housed in the collections of the Museo Paleontologico Egidio Feruglio (MPEF), Trelew, Argentina. The distribution of colonizing organisms in fern tissue was measured by superimposing a 200 µm x 200 µm grid onto the cross section of the rhizome (Fig. 1a). At each intersection of the grid, we recorded the type of fern tissue and the presence and type of colonizers. This yielded 3820 data points for the entire rhizome cross section. Of these, 252 data points included colonizing organisms (see Table 1).

# **Results**

## The host fern

The single anatomically-preserved osmundaceous rhizome (MPEF-Pb 9299) was collected from a newly discovered early Eocene locality of the Tufolitas Laguna del Hunco, La Huitrera Formation (see geologic setting for details), Argentine Patagonia (NW Chubut Province). At other sites, this formation has yielded a diverse compression flora that includes fertile osmundaceous foliage (*Todea amissa* M. Carvalho – see geologic setting for details). The rhizome, a fragment ca. 20 cm tall x 7.5 cm in diameter, shows all the features typical of osmundaceous fern stems: upright habit, characteristic dictyostele and dense persistent leaf bases with adaxially concave xylem strands, sclerenchymatous rings, and rhomboidal parenchymatous wings (Eames, 1936). The biota hosted by this rhizome includes epiphytic bryophytes, diverse fungi, and arthropods (coprolites).

## Rhizome epiphytes

More than 100 small leafy shoots are found, primarily along the outer perimeter of one side of the rhizome, but also between leaf bases elsewhere along the rhizome (Fig. 1a). These

shoots are up to 3.75 mm long and 230-410  $\mu\text{m}$  in diameter. They exhibit pinnate branching, with branches  $> 200 \mu\text{m}$  long, diverging at 450-850  $\mu\text{m}$  intervals (Fig. 2c). Stems are 30-180  $\mu\text{m}$  in diameter, comprised entirely of isodiametric to oval parenchyma cells 10-22  $\mu\text{m}$  across and 55-78  $\mu\text{m}$  long (Fig. 2c). Leaves are two-ranked and attached at 10-45  $\mu\text{m}$  intervals (Fig. 2a). Incompletely preserved, they are at least 490  $\mu\text{m}$  long, lack a midrib, and are inserted at 30-40° angles (Fig. 2a). Their thickness (7.5-12.5  $\mu\text{m}$ ) indicates that they are probably unistratose.

The small size of these plants and their lack of conducting tissues indicate that they are bryophytes. The only bryophyte group that combines pinnately branched gametophytes with two-ranked leaves that are unistratose, lack a midrib, and are inserted at wide angles to the stem are leafy liverworts (Schofield, 1985). The incomplete preservation of the leaves, which typically provide taxonomically informative characters among liverworts, precludes a narrower systematic placement of these plants.

In addition, a small root was found in the detritus at the periphery of the rhizome (Fig. 1a). The root is 0.7 mm in diameter and has a diarch protostele ca. 100  $\mu\text{m}$  wide (Fig. 2d). Secondary xylem with narrow (10-21  $\mu\text{m}$ ) tracheids (Fig. 2d) comprises ca. 75 % of the root; some bark is also preserved (Fig. 2d). The diarch primary xylem and high proportion of secondary xylem lacking vessels are features typical of gymnosperms (Esau, 1965).

## Fungi

Fungal hyphae are abundant in highly degraded parts of the rhizome and in surrounding plant detritus (Fig. 1a, 2l). They fall into two types: (1) smaller, apparently aseptate hyphae 1.5-2.0  $\mu\text{m}$  in diameter; and (2) larger, septate hyphae 3.0-5.0  $\mu\text{m}$  in diameter (Fig. 2l). The latter have septa spaced at 21-22  $\mu\text{m}$ ; clamp connections were not observed.

Darkly pigmented, round to oval cerebriform microsclerotia are also abundant in highly degraded parts of the rhizome and in the associated plant detritus (Fig. 1a). The microsclerotia are 42-50  $\mu\text{m}$  in diameter and composed of isodiametric to oval cells 4-12  $\mu\text{m}$  in size (Fig. 2f). These microsclerotia are similar in size and morphology to cerebriform microsclerotia described in the roots of *Eorhiza arnoldii* Robison et Person from the Eocene of Canada, which were attributed to dark septate endophytes, a lineage of dematiaceous ascomycetes (Klymiuk, Taylor & Taylor, 2013b).

Five other types of dispersed fungal reproductive structures are present in detritus associated with the rhizome (Fig. 1a, 2g-k). These reproductive structures are multicellular (three to eight celled), uniseriate, more-or-less linear spores lacking obvious pores (Fig. 2); four of the five types are preserved with narrow stalks (Fig. 2g, 2h-k). A first type consists of stalked, three-celled spores (Fig. 2g) ca. 15  $\mu\text{m}$  long x 6  $\mu\text{m}$  wide. The apical cell is rounded, 4  $\mu\text{m}$  long x 6  $\mu\text{m}$  wide. The middle cell is smaller, rectangular, 3  $\mu\text{m}$  long x 6  $\mu\text{m}$  wide. The basal cell is >10  $\mu\text{m}$  long and 6  $\mu\text{m}$  wide, tapering basally into a stalk 4  $\mu\text{m}$  wide. Type two includes three celled, stalked spores roughly elliptical in shape, ca. 40  $\mu\text{m}$  long and up to 16  $\mu\text{m}$  wide (Fig. 2k). The apical cell is shaped like a truncated ellipse, 18  $\mu\text{m}$  long and 16  $\mu\text{m}$  wide. The subapical cell is rectangular, 11  $\mu\text{m}$  long x 16  $\mu\text{m}$  wide. The basal cell is trapezoidal, 6  $\mu\text{m}$  long and 13  $\mu\text{m}$  wide apically, tapering to 6  $\mu\text{m}$  basally. The stalk tapers to 4  $\mu\text{m}$ . Type three consists of elongate, stalked, 7- or 8-celled spores ca. 35  $\mu\text{m}$  long and 6  $\mu\text{m}$  wide (Fig. 2h). Cells, except for the basal and apical ones, are rectangular, 3-5  $\mu\text{m}$  long x 6  $\mu\text{m}$  wide. The apical cell is rectangular-trapezoidal and slightly smaller, 2  $\mu\text{m}$  long x 5  $\mu\text{m}$  wide. The basal cell is also smaller, rectangular-trapezoidal, 3.5  $\mu\text{m}$  long x 4  $\mu\text{m}$  wide. The stalk tapers to 2  $\mu\text{m}$ . Type four is the most abundant fungal spore, three-celled, stalked and spatulate, ca. 25-30  $\mu\text{m}$  long and 15  $\mu\text{m}$  wide (Fig. 2j). The apical cell is round, 13-17  $\mu\text{m}$  in diameter. The middle cell is small and rectangular, 5-7  $\mu\text{m}$  long x 7-8  $\mu\text{m}$  wide. The basal cell is rectangular-trapezoidal, 8  $\mu\text{m}$  long and 7  $\mu\text{m}$  wide apically, tapering to 5  $\mu\text{m}$  basally. The stalk tapers to 3-4  $\mu\text{m}$ . Type five consists of slightly curved chains of five cells, ca. 38  $\mu\text{m}$  long and 9  $\mu\text{m}$  wide (Fig. 2i). The apical cell is rounded, 8  $\mu\text{m}$  long and 6  $\mu\text{m}$  wide. The sub-apical cell is inflated, 7  $\mu\text{m}$  long x 9  $\mu\text{m}$  wide. The third cell is rectangular-trapezoidal, 7  $\mu\text{m}$  long x 5  $\mu\text{m}$  wide, tapering to 4  $\mu\text{m}$ . The fourth cell is rectangular, 6  $\mu\text{m}$  long x 4  $\mu\text{m}$  wide. The basal cell is square, 4  $\mu\text{m}$  across.

In terms of potential taxonomic affinities, type one spores compare in overall morphology to smaller members of the dispersed fossil spore genus *Diporicellaesporites* Elsik, especially *D. minisculus* Sheffy et Dilcher, but the pores diagnostic of this genus (Kalgutkar & Jansonius, 2000) are not observable in the Argentinean material. Type two and four spores are comparable to species of the dispersed spore genus *Brachysporites* Lange et Smith, whose multicellular, usually spatulate spores resemble conidia of the extant dematiaceous ascomycete genus *Brachysporium* Saccardo (Kalgutkar & Jansonius, 2000; Taylor, Krings & Taylor, 2015). Within *Brachysporites*, type two spores are most similar to *B. atratus* Kalgutkar, while type four

spores are most similar to *B. pyriformis* Lange et Smith (Kalgutkar & Jansonius, 2000). Type three spores are comparable to conidia of the extant magnaporthaceous ascomycete *Clasterosporium* Schwein. (Kalgutkar & Jansonius, 2000); the extinct *C. eocenicum* Fritel et Viguiet is especially similar to type three spores, although the latter are slightly smaller. Type five spores are comparable to the conidia of the extant pleosporaceous ascomycete *Curvularia* Boedijn based on their size, curved shape, and inflated subapical cell (Elsik, 1993).

Overall, the fungal reproductive structures documented on the Patagonian rhizome are comparable with those of several ascomycete lineages, including Dematiaceae (microsclerotia and two of the spore types), Magnaporthaceae and Pleosporaceae (Elsik, 1993; Kalgutkar & Jansonius, 2000; Klymiuk, Taylor & Taylor, 2013b). Septate hyphae lacking clamp connections frequently found in the vicinity of these reproductive structures are consistent with ascomycete affinities. Given that all this fungal material was found in detritus or very degraded plant material (Fig. 1a), these fungi were probably saprotrophs, rather than parasites or endophytes.

### Coprolites

Small, round to ovoid coprolites occur towards the periphery of the rhizome, in excavations of the parenchymatous mesophyll, fiber band, and vascular tissue (Fig. 1a, 2e). Coprolites also occur externally to fern tissues, in highly degraded portions of the rhizome (Fig. 1a). They have smooth surfaces and are 23-260  $\mu\text{m}$  in diameter, composed of angular cell-wall fragments and opaque bodies (Fig. 2e). Based on their size, shape and texture, the excavations and coprolites were probably produced by oribatid mites (Labandiera, 1998; Kellogg & Taylor, 2004; McLoughlin and Bomfleur, 2016).

### Degraded cell contents

The degraded portions of the rhizome have groups of cells that are filled with small, spherical structures 2-6  $\mu\text{m}$  in diameter (Fig. 2m). These structures occur in cells of all tissue types (parenchymatous leaf base mesophyll, fiber band and vascular tissue) (Table 1). Their perfectly circular shape, tendency to completely fill cells, and variable size indicate that these structures are not microorganisms. Instead, they probably represent a particular type of cell content degradation and aggregation due to the fossilization processes, also seen in the Early Devonian Rhynie chert plants (Michael Krings, personal comm., 2017).

# Discussion

## Distribution patterns

It is unclear whether the fern rhizome was living at the time of permineralization. Nevertheless, a variety of biotic interactions, involving arthropods, liverworts, fungi and vascular plants, were clearly occurring, covering the rhizome in several kinds of life (Fig. 1a) just like extant osmundaceous rhizomes (Fig. 1b). The distribution and frequency of each kind of organism associated with the rhizome by tissue type (Fig. 2n; Table 1) show that most associated organisms are much more abundant in the more degraded region of the rhizome (Fig. 1a). Liverworts and fungi in detritus are found primarily external to the fern tissues, and secondarily in some of the most degraded tissues near the periphery of the rhizome (Fig. 1a, 2n). Coprolites also occur in all types of tissue, as well as externally to some of the most degraded leaf bases, indicating that the arthropods that produced them did not have strong preference for lignified or parenchymatous tissues (Fig. 1a, 2n).

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

A similar community of organisms has been described associated with an exceptionally well preserved *Osmunda pulchella* Bomfleur, G. Grimm et McLoughlin rhizome from the Jurassic of Sweden (Bomfleur, McLoughlin & Vajda, 2014; McLoughlin & Bomfleur, 2016). Like the Patagonian rhizome, this Jurassic community included fungi, oribatid mites (coprolites) and epiphytes. However, in the case of the *Osmunda pulchella* community, the epiphytes are exclusively vascular (lycopsid roots, fern leptosporangia, spores). Additionally, fungal material is more abundant and diverse in the Patagonian rhizome, probably correlated with higher proportions of decomposed tissues. The richness of both these communities associated with osmundaceous rhizomes suggests that other permineralized fern rhizomes may also host diverse associations of organisms and serve as models for understanding biotic interactions in deep time.

## Significance of the leafy liverwort fossils

Given the sparse fossil record of liverworts (Oostendorp, 1987; Tomescu, 2016; Tomescu, A. M. F. unpublished data), it is not surprising that these tiny epiphytes represent the first report of fossil leafy liverworts from South America. *Marchantites hallei* Lundblad

(Lundblad, 1955), a thalloid liverwort from the Early Cretaceous of Argentina, is the only other unequivocal fossil liverwort known from South America (Oostendorp, 1987; Tomescu, A. M. F. unpublished data). Additionally, the liverworts described here are the first epiphytic leafy gametophytes in the fossil record. All other fossils of epiphytic bryophytes are moss protonemata described on angiosperm leaves (Mägdefrau, 1956; Selkirk, 1974; Barclay et al., 2013).

## Conclusions

The complex community of organisms associated with the Patagonian osmundaceous fern rhizome allows a glimpse of a tiny, ancient ecosystem centered around a single host plant. This 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 coprolites. Understanding of complex interactions in fossil biotas, including detailed insight into component communities like those of this Patagonian rhizome, is needed to paint a more complete picture of life in the geologic past. In the fossil record, complex interactions of plants have only been characterized in uncommon instances (e.g., Rhynie chert, the petrified forest of Chemnitz; Rössler, 2000; Taylor et al., 2004). In contrast to these rare occurrences, fossil osmundaceous ferns and the communities they may harbor are widespread geographically and stratigraphically (Stewart & Rothwell, 1993; Taylor, Taylor & Krings, 2009). Osmundaceous ferns can be traced back into the Paleozoic (Miller, 1967; Miller, 1971; Stewart & Rothwell, 1993; Taylor, Taylor & Krings, 2009) at a time when ecological networks were becoming canalized (DiMichele et al., 1992). Furthermore, osmundaceous morphology has been in stasis since the Paleozoic (Eames, 1936; Stewart & Rothwell, 1993). As such, osmundaceous rhizomes represent a distinctive ecological niche, unchanged since the Permian, and acts as a hub for interactions between plants, fungi, and animals, which can also be studied in the modern biota and can be sampled systematically and consistently across all occurrences, fossil and extant. Because of the scale of these interactions (centimeter to millimeter), entire in situ tiny ecosystems and the interactions within can be studied directly in fossil specimens. To date, permineralized osmundaceous rhizomes have yielded evidence for plant interactions with invertebrates (Schopf, 1978; Tidwell & Clifford, 1995; Bomfleur, McLoughlin & Vajda, 2014).

and fungi (Kidston & Gwyne-Vaughan, 1907; Gould, 1970; Bomfleur, McLoughlin & Vajda, 2014). These occurrences confirm 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, they provide a paleoecological model system for exploring plant biotic interactions across geologic time. Given the diversity of interactions recently recorded in La Huitrera Formation and the Jurassic of Sweden, as well as the abundance of osmundaceous rhizomes in the fossil record (Miller, 1967; Miller 1971; Taylor, Taylor & Krings, 2009), we predict that continued exploration will reveal additional aspects of the biotic networks centered around these important repositories of ecological data from the geologic past.

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**Table 1**(on next page)

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

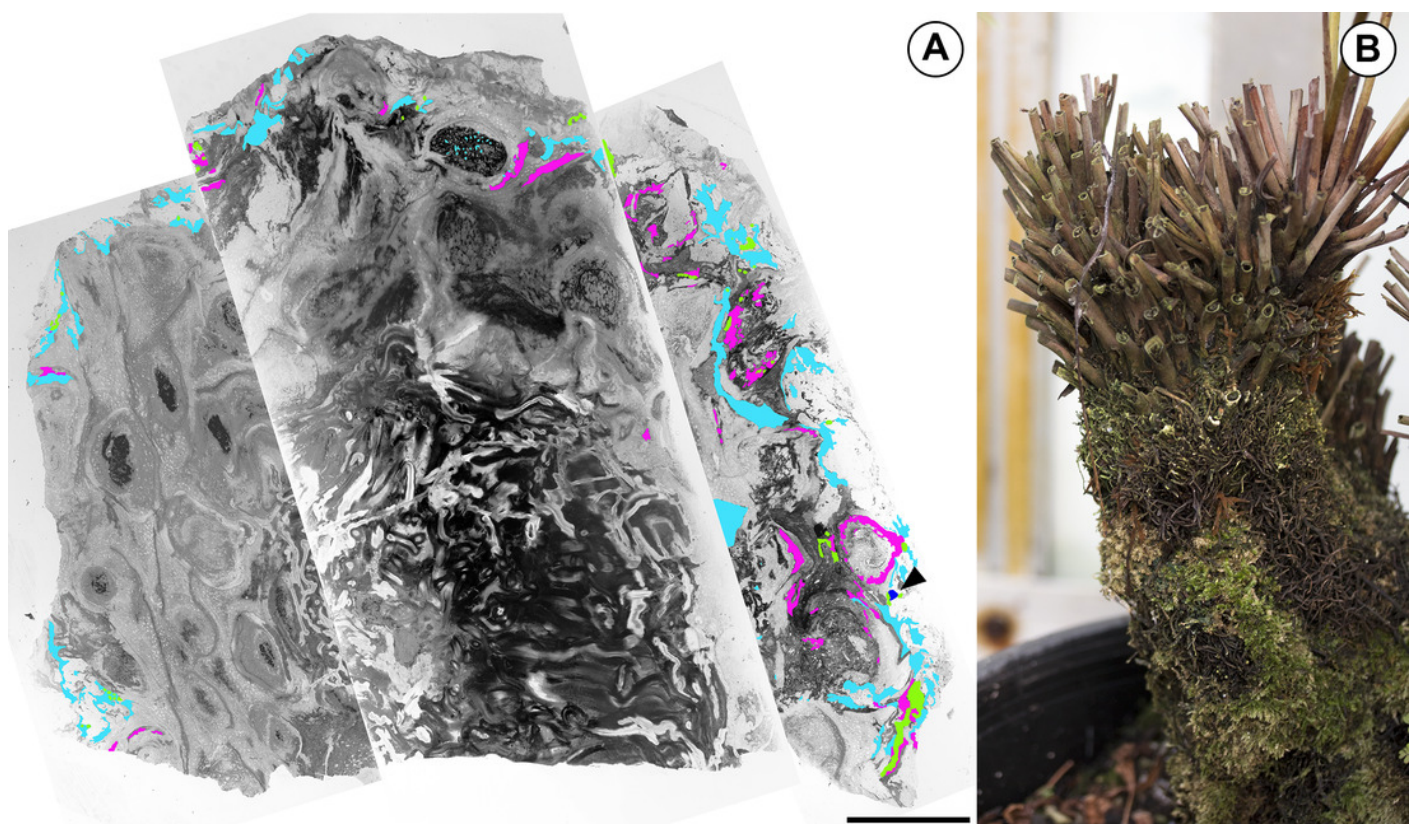
Table 1. Distribution of types of organisms colonizing the Patagonian osmundaceous rhizome (data point counts).

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  $\mu\text{m}$ ; f 25  $\mu\text{m}$ ; g-k, m 5  $\mu\text{m}$ ; l 2.5  $\mu\text{m}$ .



