

A gondwanan Jurassic bryoflora? Anatomically preserved bryophytes in geothermal paleoenvironments from the Jurassic of Patagonia, Argentina

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ABSTRACT

The Deseado Massif, which is located in the western part of the Santa Cruz Province, Argentina, contains numerous hot spring deposits related to the final stages of the Bahía Laura Complex. The aim of this study is to analyze the first Jurassic deposits with permineralized bryophytes at La Bajada hot spring-related locality, expanding the diversity of Jurassic bryophytes with anatomical preservation. > 200 fossiliferous petrographic thin sections were examined, leading to the discovery of four bryophyte morphotypes of leafy and thallose gametophytes. Detailed comparisons between each morphotype and extant and extinct bryophytes were carried out. The morphotypes described here may have various phylogenetic affinities, based on the latest comprehensive phylogenetic analyses of extant bryophytes. Although morphotypes described here do not represent the oldest representative for the lineages they represent, each of the studied fossils has a consistent set of diagnostic characters that relates them to specific nodes within bryophyte phylogeny. Moreover, the affinities of morphotype A with Marchantiales and Neohodgsoniales suggest affinities with the clade that is composed of these two orders together with Sphaerocarpaceae. Affinities of morphotypes B, C and D are more ample and related to different orders including within Bryophyta sensu stricto.

1. Introduction

With more than 20,000 species described in modern floras (Shaw et al., 2011), bryophytes (i.e., Bryophyta s.s., Marchantiophyta and Anthocerotophyta) are a very diverse group of land plants. Bryophytes are widely distributed, inhabiting all ecosystems, except for the marine realm (Schofield, 1985; Vanderpoorten and Goffinet, 2009; Goffinet and Buck, 2013). Evidence suggests bryophytes were probably the first plants to colonize land and endure the early land Earth conditions (Graham et al., 2014) and that they contributed to the development of the first organic soils (Glime, 2017). Bryophytes are generally considered the most ancient lineages of land plants and, likewise, the first true plants (Glime, 2017), but more recent studies have challenged this understanding of the group (e.g. Harris et al., 2022). Phylogenetic

relationships among bryophytes and between these and tracheophytes remain controversial (e.g. Morris et al., 2018; for a review see Cox, 2018). Several studies have supported the monophyly of extant bryophytes (e.g. Cox et al., 2014; Wickett et al., 2014; Puttick et al., 2018; de Sousa et al., 2019; Cole et al., 2019; Bell et al., 2020; Harris et al., 2022; Bechteler et al., 2023). However, a growing body of phylogenetic evidence from morphological and molecular studies now supports the view that liverworts and mosses form a clade, “the setaphytes”. Relationships between the setaphytes and the two other lineages of land plants (vascular plants and hornworts), remain uncertain (e.g. Renzaglia and Garbary, 2001; Rensing, 2018; Puttick et al., 2018; Bell et al., 2020).

Historically, the bryophyte fossil record has been considered sparse (e.g. Gray and Lawson, 1985; Edwards et al., 1998; Wellman, 2010). Recent reviews of bryophyte macrofossils and mesofossils revealed that

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the oldest unequivocal record of this group dates back to the Devonian, with fossils becoming increasingly more diverse and amply distributed geographically from the Permian on (Tomescu et al., 2018; Ignatov and Maslova, 2021). Tomescu et al. (2018) reported 449 pre-Neogene fossil bryophyte types, most of which are impressions/compressions (224 taxa; e.g. Krassilov, 1973; Chandra, 1995; Cantrill, 1997; Cladera et al., 2007) and amber inclusions (172 taxa; e.g. Mamontov et al., 2015; Ignatov et al., 2016; Heinrichs et al., 2017). Other less common bryophyte fossils include exceptionally preserved fossils in the form of cuticles (40 taxa; e.g. Oostendorp, 1987; Maslova et al., 2016), permineralizations (20 taxa; e.g. Smoot and Taylor, 1986; Vera, 2010; Shelton et al., 2016; Tomescu et al., 2018 and references therein) and charcoalifications (3 taxa; e.g. Konopka et al., 1997, 1998).

Mesozoic bryophytes are represented by 141 records, which includes 40 from the Jurassic that consist of 25 liverworts (19 thalloid liverworts, 6 leafy liverworts) and 15 mosses. These records indicate that every subclass of liverwort with extant representatives (i.e., Marchantiidae, Jungermanniidae, Pelliidae, Metzgeriidae) can be traced back to the Jurassic. Furthermore, the Mesozoic moss fossil record includes representatives of Hypnanae, the most diverse superorder of extant bryophytes (ca. 4500 species) (Ignatov and Maslova, 2021). The vast majority of these Mesozoic fossils are preserved as compression/impressions (e.g., Oostendorp, 1987; Wu and Wang, 2000; Ociepa, 2007), which primarily preserve only external morphology. Given this paucity of anatomical information on Mesozoic bryophytes, permineralizations represent a unique opportunity for the preservation of complementary sets of features that would enable more precise taxonomic placement of

fossil specimens (e.g., Shelton et al., 2015; Bippus et al., 2017; Savoretti et al., 2018). An initial survey and study of the chert at the Jurassic geothermal localities in the Deseado Massif in the Santa Cruz province (Argentina) has revealed several three-dimensionally preserved bryophyte fossils, including the first anatomically preserved bryophyte from the Jurassic, *Heinrichiella patagonica* (Subphylum Bryophytina; Bippus et al., 2019).

The aim of this study is to analyze the bryophyte content at the most diverse assemblage of bryophytes uncovered over the course of this investigation (La Bajada locality), thereby expanding the Jurassic diversity of bryophytes with preserved anatomical features.

2. Material and methods

2.1. Geologic settings and locality

The studied samples were collected at the La Bajada Jurassic hot spring locality of the Bahía Laura Complex, which is located in the western part of the Deseado Massif, Santa Cruz Province, Argentina (Fig. 1, see Guido and Campbell, 2011). The Deseado Massif is an extensive region (60,000 km²) with abundant volcanic rocks deposited during the middle to upper Jurassic (178–151 million years ago; Pankhurst et al., 2000) in relation to the breakup of Gondwana and the beginning of the opening of the South Atlantic Ocean. Rocks of the Bahía Laura Complex are part of the Chon Aike SLIP (silicic large igneous province), which ranges from Patagonia to Antarctica (Pankhurst et al., 1998), and is composed of bimodal (andesite and rhyolite) calc-alkaline,

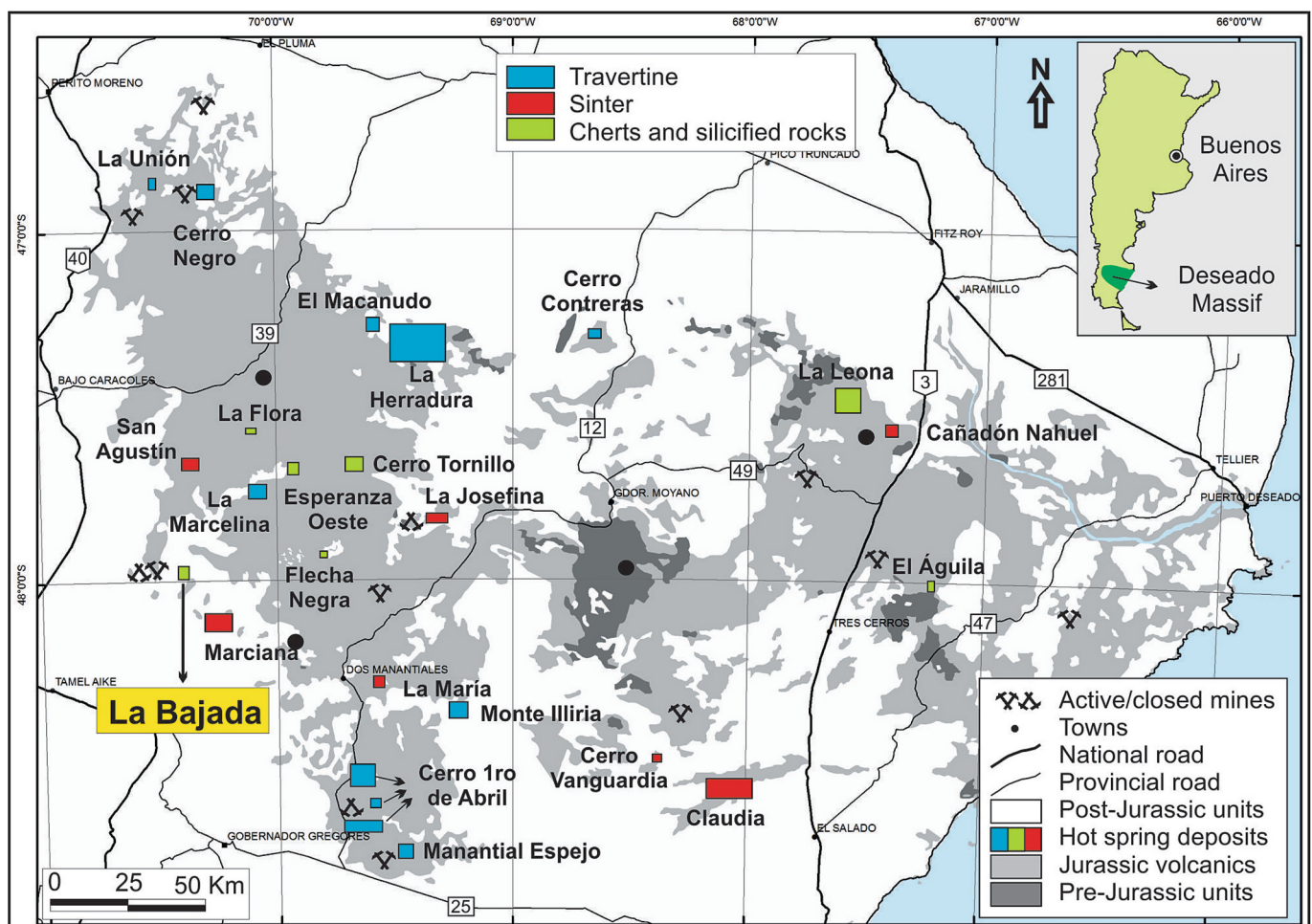


Fig. 1. Deseado Massif (Patagonia, Argentina) summarized geological map with Jurassic hot spring deposit localities, and detail of the area indicating the location of the chert-bearing bryophytes fossil deposits at La Bajada (modified from Guido and Campbell, 2019).

volcanic rocks.

Jurassic extensional volcanism at the Deseado Massif includes large hydrothermal processes, which produced gold and silver-bearing deposits with nine active mines, and hot spring-related deposits discriminated into sinter, travertine and cherts and silicified rocks (Schalamuk et al., 1997; Guido and Campbell, 2011; Guido and Campbell, 2019). Some of these localities, in particular sinters and cherts, comprise well-preserved fossilized organisms representing the only known fossiliferous Mesozoic hot spring deposit (Channing and Edwards, 2013).

2.2. Preparation and imaging of studied material

Four hundred chert blocks from La Bajada were cut using a Buehler PetroThin thin-sectioning machine (Buehler, Lake Bluff, IL). The exposed faces were polished to reach a thickness of $\sim 30\ \mu\text{m}$ following standard methods, and subsequently mounted on a glass slide (Hass and Rowe, 1999). Using this technique, more than 1 mm of the sample is lost to the saw kerf or abraded away to produce a single section. Because of bryophyte small size, only one thin section could be produced of each bryophyte gametophyte preserved at La Bajada. Therefore, while these fossils preserve rich anatomical information, only extremely coarse information regarding overall morphology is preserved for each bryophyte specimen.

Plants within rock sections were examined using a dissecting microscope and incident light, revealing mosses and liverworts gametophytes. Slides were observed using transmitted light microscopy. All images were taken with a Leica DFC450 C camera connected to a Leica DM2500 compound light microscope. At higher magnifications, multiple images of the same structure of interest were taken at different focal planes to compose an image with greater depth of focus, following an image-stacking technique (Bercovici et al., 2009). In some cases, several partially overlapping images were merged to create a single high-quality image. This technique was applied using Adobe Photoshop CS6. The specimens and thin sections are housed at the Museo Regional Padre Molina of Río Gallegos (Santa Cruz Province, Argentina) under accession numbers MPM-PB 16066, MPM-PB 16071, MPM - PB 16073.

2.3. Taxonomic treatment

We follow the bryophyte classification proposed in Goffinet and Shaw (2009), with modifications proposed by Bechteler et al. (2023). Phylogeny shown in figures corresponds to the proposal of Bechteler et al. (2023).

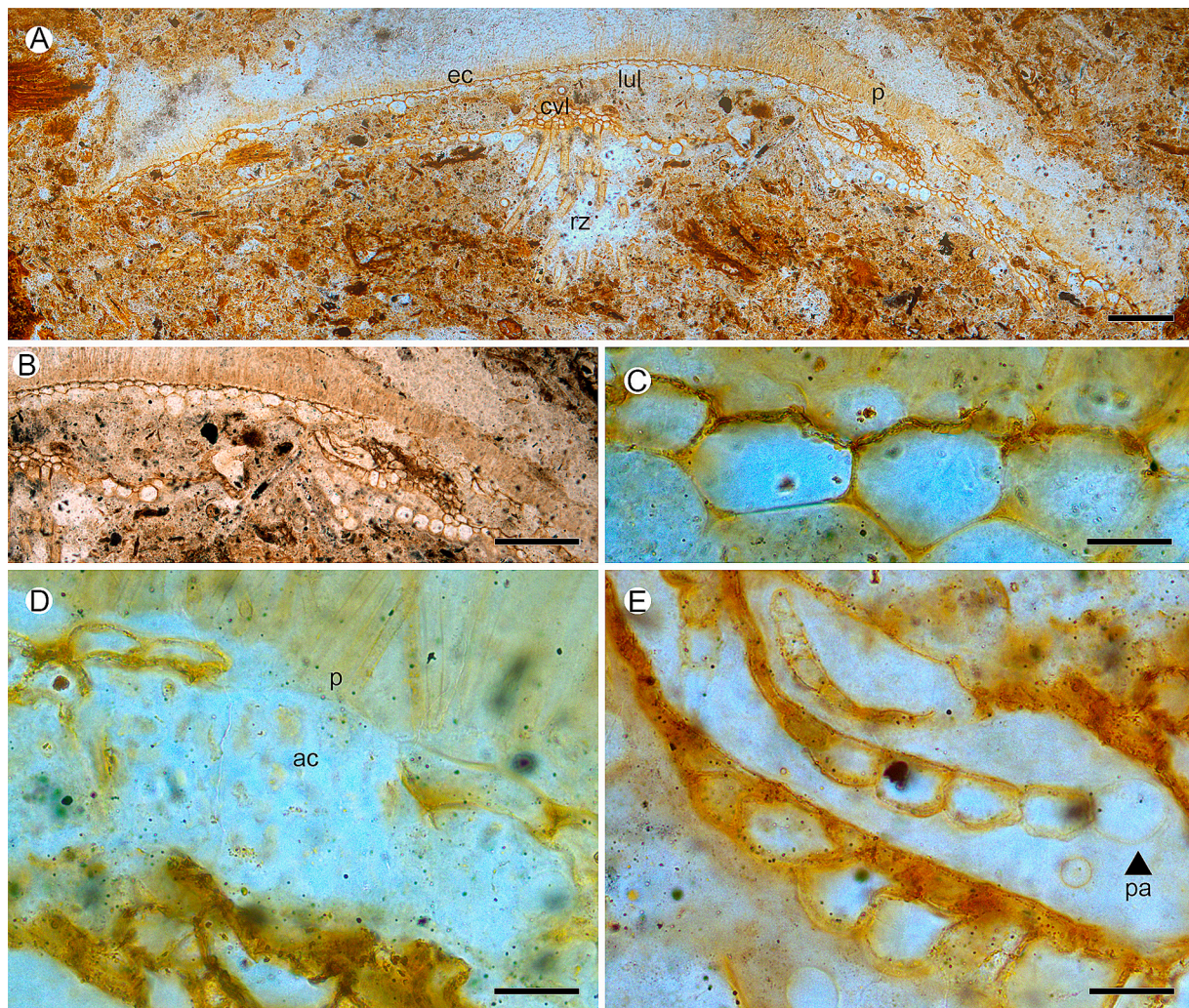


Fig. 2. Morphotype A. Thallose bryophyte morphotype from La Bajada Locality. A General view of thallus. B. Section showing the inner thallus organization into an upper lax layer and a compact ventral layer. C. Detail of epidermal cells. D. Detail of dorsal surface, showing pore and air chamber. E. Thallos ventral surface showing scales / Scale bar: A. 200 μm , B. 20 μm , C. 200 μm , D. 20 μm , E. 20 μm / ep: epidermal cells; lul: lax upper layer; cvl: compact ventral layer; p: pore; ac: air chamber; rz: rhizoids; pa: papilla of a scale.

3. Results

From the ~200 rock sections inspected, four bryophyte morphotypes of leafy and thallose gametophytes were recognized. Each morphotype is taxonomically placed and described in detail below.

Taxonomic descriptions

Phylum: MARCHANTIOPHYTA Stotler & Crand.-Stotl.

Class: MARCHANTIOPSIDA Gonquist, Takht & W. Zimm.

Subclass: MARCHANTIIDAE Engl.

Morphotype: A

Locality: Provincial Road 79 (coordinates 47°57'54.8"S 70°24'49.4"W), from La Aragonesa farm to El Frigorífico farm, Santa Cruz province, southern Argentina (Fig. 1).

Material: MPM - PB 16073.

Stratigraphic horizon: Massive gray to orange chert, uppermost part of the Bahía Laura Jurassic volcanic Complex (Fig. 1); upper Jurassic.

Diagnosis: Morphotype A is recognizable based on the following combination of features: 1) thallose gametophyte, 2) complex thallus structure, 3) pores present on dorsal surface and, 4) scales and rhizoids on the ventral surface.

Description: Morphotype A consists of a well-preserved thallose gametophyte (Fig. 2A, Appendix A). The thallus is ca. 3 mm long, 0.2 mm wide. In cross section it is possible to recognize epidermal cells ($x: 29 \mu\text{m} \times 22 \mu\text{m}$), an inner tissue organized in two layers (a lax upper layer and a more compact ventral layer) (Fig. 2B–C), the dorsal surface with pores (epidermal cells: $20 \mu\text{m} \times 9 \mu\text{m}$) with air chambers (Fig. 2D), and ventral surface with scales and smooth rhizoids (Fig. 2E). The outer cells of scales are thin walled cells that correspond to papillae (Fig. 2E). Interspersed with scales there also are tubular structures that are circular in cross section that probably correspond to rhizoids.

Comparisons between Morphotype A and extant bryophyte lineages: The presence of scales, unicellular rhizoids, and absence of lignified vascular tissues suggests that Morphotype A represents a gametophyte of a thalloid liverwort (Hässel de Menéndez, 1963; Crandall-Stotler and Stotler, 2000). The overall morphology of this specimen shows a superficial resemblance to fern gametophytes. However, this affinity can be discarded since mature fern gametophytes (in the multistratose stage) lack scales or unicellular rhizoids, and lack pores in their dorsal surface (e.g. Tanco et al., 2008; Escamilla-Aquino et al., 2008).

Many members of the Marchantiidae, Pellidae and Metzgeriidae have thallose gametophytes. However, Pellidae and Metzgeriidae mostly have anatomically simple thalli without air chambers (Crandall-Stotler and Stotler, 2009; Cole et al., 2019), and only in subclass Marchantiidae do gametophytes develop anatomically complex thalli (gametophyte with dorsal pores, an upper green, chambered tissue and a lower solid tissue, ventral scales, and two kinds of rhizoids) (Crum, 2001; Hässel de Menéndez, 1963). The diversity of living forms within Marchantiidae is organized in four orders: Blasiales, Neohodgsoniales, Sphaerocarpaceae, Marchantiales (Flores et al., 2021; Söderström et al., 2016; Bechteler et al., 2023).

Thalloid gametophytes of Blasiales are quite different from the fossil specimen because they are anatomically simple, with conspicuously defined wings and midrib (Schofield, 1985; Crandall-Stotler and Stotler, 2009), whereas the thallus of Morphotype A is anatomically complex and lacks a clear distinction between midrib and wings. Affinities with the Sphaerocarpaceae can be discarded because this order develops structurally simple thalli (Crandall-Stotler and Stotler, 2009), notably different from the anatomically complex thalli of Morphotype A.

Among complex thallose Marchantiidae (sensu Flores et al., 2021), Marchantiaceae is more similar to the fossil specimen than Ricciaceae. In Ricciaceae gametophytes are greatly simplified (e.g. in *Riccia* and *Ricciocarpus*) and pores are rudimentary or absent (Hässel de Menéndez, 1963; Schofield, 1985). The anatomical features of the fossil gametophyte are similar to the extant genus *Marchantia* (see fig. 4-A in Shimamura, 2015). However, Neohodgsoniales also share several features with the fossil. Specifically, the thallus is differentiated into layers, with

the upper layer containing air chambers, epidermis with air pores, ventral scales, and only smooth rhizoids (Long, 2006).

Ultimately, the combination of characters observed in Morphotype A suggest affinities with Marchantiidae. The fossil is similar to two orders within this class, Marchantiales and Neohodgsoniales. Ongoing studies of the La Bajada fossils could potentially lead to the discovery of additional specimens that may preserve additional features. Such additional features would be necessary to further refine the taxonomic assignment for this morphotype beyond Marchantiidae (e.g., morphology of pores, rhizoids and the chlorophyllous cells) (Hässel de Menéndez, 1963; Crandall-Stotler and Bartholomew-Began, 2007).

Comparison between Morphotype A and other anatomically-preserved fossil bryophytes: The Apple Bay bryophyte flora described by Tomescu (2016) includes one fossil specimen that exhibits several features characteristic of thalloid liverworts. For instance, as in Morphotype A, the cellular organization of the thallus into an upper lax region and a more compact basal region resembles the anatomy of a complex thalloid liverwort. In addition, the upper surface of this Cretaceous fossil preserves groups of irregularly-arranged small cells with thin walls that could represent remnants of a photosynthetic layer that would probably have been protected by an upper epidermis (not preserved), if it resembles extant complex thalloid liverworts. On the lower surface of the specimen, rhizoid bases are recognized, attached to small thin-walled cells representing a lower epidermis. The absence of important features like scales and air pores in the Apple Bay specimen are critical differences between this specimen and Morphotype A.

Shuklanites deccanii Singhai (1964) and *Notothylites nirulai* Chitaley et Yawale (1980), both from the Late Cretaceous of India, possibly correspond to sporophytes (capsule, bulbous foot, spores and pseudolaters) embedded in a thallus (Singhai, 1964, 1973; Chitaley and Yawale, 1980) tentatively assigned to Anthocerotophyta (Singhai, 1964; Chitaley and Yawale, 1980). Among the morphotypes described here only Morphotype A is remotely similar as this morphotype corresponds to a thalloid form, although it is known exclusively on the base of vegetative features. Based on gametophytic features, *Shuklanites deccanii* differs from Morphotype A in the structure of its thallus, which is simple and does not present air chambers (see Singhai, 1973). In *Notothylites nirulai* several differences with Morphotype A can be observed. For example, *N. nirulai* has a triangular thallus without a distinct midrib and several thick cells like rhizoids but this feature is not completely preserved. Additionally, structures similar to scales are absent (Chitaley and Yawale, 1980).

Phylum: BRYOPHYTA Schimp.

Superclass: V

Class: BRYOPSIDA Pax.

Morphotype: B

Locality: Provincial Road 79 (coordinates 47°57'54.8"S 70°24'49.4"W), from La Aragonesa farm to El Frigorífico farm, Santa Cruz province, southern Argentina (Fig. 1).

Material: MPM - PB 16066.

Stratigraphic horizon: Massive gray to orange chert, uppermost part of the Bahía Laura Jurassic volcanic Complex (Fig. 1); upper Jurassic.

Diagnosis: Morphotype B can be recognized based on the following combination of features: 1) leaves with a single, strong and heterogeneous costa, 2) a leaf lamina composed of mammillose-bulging cells and, 3) a stem lacking a central strand.

Description: This morphotype is known from a single thin section of a gametophyte shoot (1.1 mm in diameter) represented by one unbranched stem and two associated leaves (Fig. 3A, Appendix A). The stem is incompletely preserved as an oblique transverse section of 0.8 mm long $\times$ 0.3 mm wide (Fig. 3B). Only the outermost tissues of the stem are preserved and they are composed of isodiametric cells. One of the associated leaves is well preserved in transverse section (Fig. 3A, C, E). The lamina is unistratose and consists of isodiametric, bulging cells ($x: 13 \mu\text{m}$ tall $\times$ $11 \mu\text{m}$ wide) (Fig. 3D), which bear low mammillae on their adaxial and abaxial surfaces. The leaf has a strong costa which is plano-convex in section. The costa consists of four anatomically distinct layers

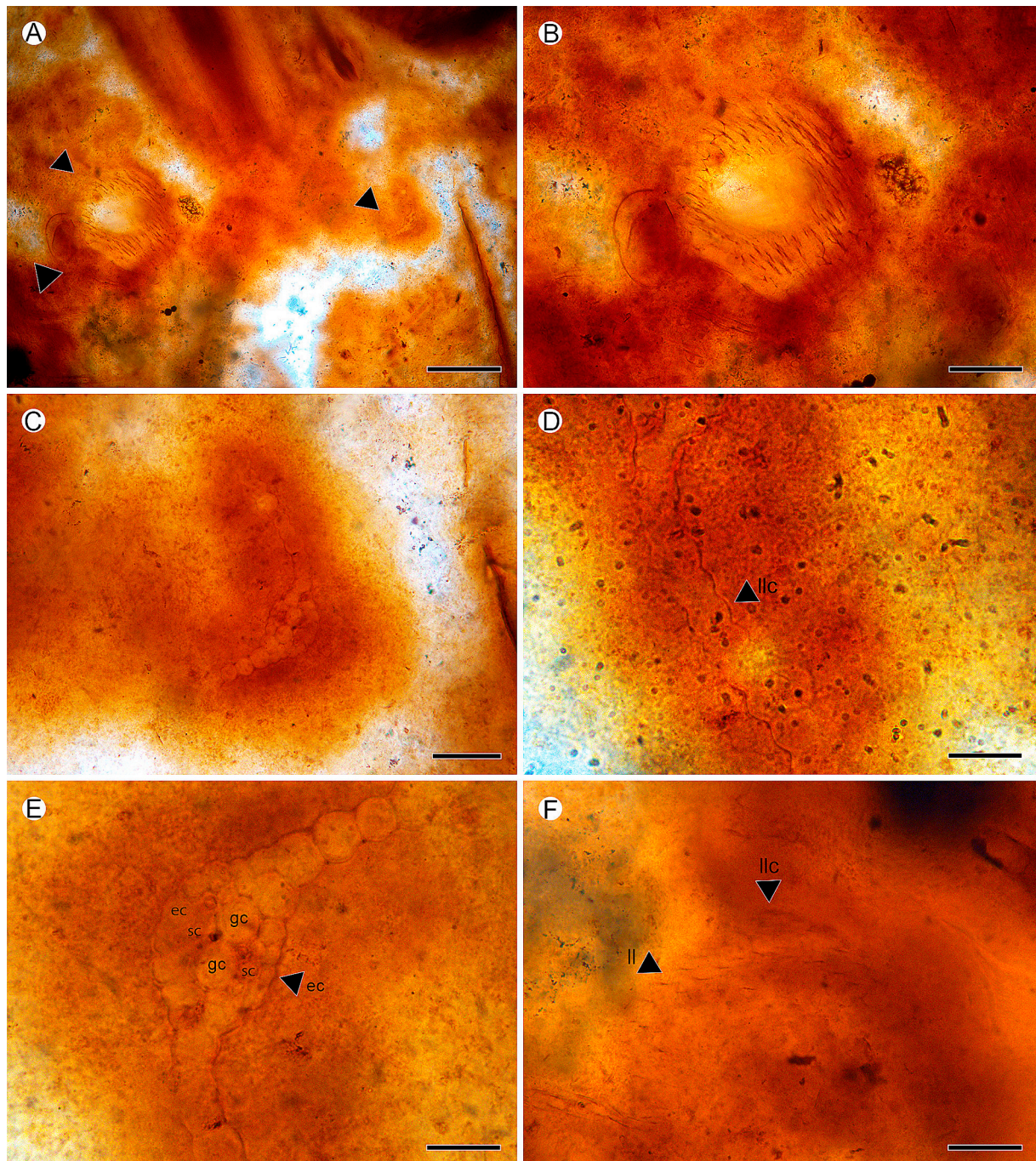


Fig. 3. Jurassic moss from La Bajada Locality, Morphotype B. A. General aspect of Morphotype B shoot (arrows indicate leaves and shoot). B. Detail of stem section. C. Leaf cross section. D. Leaf lamina cross section, highlighting laminal cell shape. E. Detail of leaf costa, showing epidermis at both surfaces, abaxial and adaxial stereid bands, and two guide cells. F. Oblique section of a second incompletely preserved leaf. / Scale bars: A: 200 μ m, B: 100 μ m, C: 50 μ m, D: 20 μ m, E: 20 μ m, F: 50 μ m / gc: guide cells; ec: epidermal cells; sc: stereids cells; lc: leaf costa; llc: leaf lamina cells.

(Fig. 3E): 1) an adaxial epidermis of small cells 8 μ m in diameter, 2) adaxial and abaxial stereid bands consisting of thick walled cells, 4 μ m in diameter, with dark lumens, 3) a central layer of guide cells (13 μ m in diameter), which are circular, 4) an abaxial epidermis of isodiametric cells that are incompletely preserved (5 μ m in diameter). The other associated leaf is incompletely preserved as an oblique section (Fig. 3A, F).

Comparisons between Morphotype B and extant bryophyte lineages: The absence of lignified vascular tissues indicates that Morphotype B represents a leafy bryophyte gametophyte. Leafy gametophytes are known from two distantly related groups of bryophytes: leafy liverworts and

mosses (Gradstein et al., 2001; Goffinet and Shaw, 2009). The presence of a costa indicates that Morphotype C is a moss and not a leafy liverwort because leafy liverworts are exclusively ecostate, whereas most mosses have costate leaves (Schofield, 1985).

Individually, gametophytic features of Morphotype B are found in several groups of mosses (e.g., Zander and Eckel, 1993; Gradstein et al., 2001; Ochrya et al., 2008; Lüth, 2019a, 2019b, 2019c). Comparable morphologies are found in families distributed across the subclasses Funariidae (e.g., Encalyptaceae), Dicranidae (e.g. Ditrichaceae, Dicranaceae, Pottiaceae) and Timmiidae (Timmiellaceae).

Morphotype B shares with the Encalyptaceae unicastate leaves, a

plano-convex costa, which is anatomically heterogeneous, and a unistratose lamina (Ochyra et al., 2008; Magill, 2007). Although in this family the costa is heterogeneous, it differs from the fossil in the presence of only an abaxial stereid band, and, in some cases, there is a central group of hydroids, which is absent in the fossil specimen (Horton, 1981). *Bryobrittonia*, one of the two genera of this family, also shares with the fossil the presence of mammillose leaf cells (Vitt, 1974; Steere, 1953). *Encalypta*, the other genus in this family, has thick walled, strongly papillose laminal cells and large, branching or c-shaped papillae (Horton, 1981), which differ from the bulging-mammillose lamina cells in Morphotype B.

Several extant representatives of Subclass Dicranidae are morpho-anatomically similar to Morphotype B. The main features that Morphotype B shares with extant families of this subclass are the presence of single costate leaves with heterogeneous costa (e.g., epidermal cells, stereid bands and guide cells) and the unistratose lamina. Most similar genera are distributed within the families Pottiaceae, Ditrichaceae and Dicranaceae (Zander and Eckel, 1993; Ochyra et al., 2008).

Laminal cells of most taxa in Family Pottiaceae are typically described as papillose (e.g. Zander and Ochyra, 2001; Cano and Gallego, 2008), unlike Morphotype B, which has bulging-mammillose laminal cells. However, in this family laminal cells have superficial walls varying from completely flat or slightly convex to intensively bulged; but this feature is often masked by the high density of papillae (e.g., *Tortula*, *Weisiopsis*) (Zander and Eckel, 1993). The costa of pottiaceous mosses is heterogeneous, but within the family, the organization and cell composition of such heterogeneity varies notoriously. For example, the costal anatomy in the genus *Eucladium* (Zander and Eckel, 1993) is very similar to those in the fossil, whereas in *Phascum* (Stone, 1989) the anatomy is remarkably different. The combination of characters in Morphotype B falls within the range of morpho-anatomical variation found in the Pottiaceae and, therefore, affinities with this family are possible.

Some genera within the Ditrichales are also broadly similar to Morphotype B. These genera share with the fossil the presence of single-costate leaves with heterogeneous costa and thin-walled laminal cells that are rounded to quadrate-rectangular in cross section. However, species within this family usually have a well-defined stem central strand, whereas Morphotype B lacks a central strand. Additionally, in the Ditrichaceae leaf laminal cells are usually smooth, not bulging-mammillose, as in Morphotype B, although some species of *Ceratodon* have bulging-mammillose lamina cells; (Norris and Koponen, 1988).

In addition, the Family Timmiellaceae shares two key features with Morphotype B: 1) The presence of a single costate leaf with a heterogeneous costa and, 2) bulging-mammillose laminal cells. However, Morphotype B has laminal cells that are bulging-mammillose on both abaxial and adaxial surfaces, whereas the two extant genera in this family (i.e., *Timmiella* and *Luiseiella*) have cells adaxially bulged and abaxially flat (Inoue and Tsubota, 2014). The leaf lamina in Timmiellaceae can be unistratose (i.e. *Luiseiella*), like Morphotype B, or bistratose (i.e. *Timmiella*) (Inoue and Tsubota, 2014). Another difference between the costa anatomy of this family and Morphotype B is the presence of epidermis only ventrally in *Luiseiella*, or at both surfaces, with the adaxial epidermis bi or tri-stratose in *Timmiella* (Zander and Eckel, 1993). In contrast, the costa of Morphotype B has a unistratose epidermis on both, abaxial and adaxial surfaces.

Comparison between Morphotype B and other anatomically preserved fossil bryophytes: *Heinrichsiella patagonica* Bippus, Savoretti, Escapa, Massini et Guido (2019) from Cañadón Nahuel Locality in the northern belt (Guido and Campbell, 2011) of Jurassic chert localities in the Deseado Massif (see also Nunes et al., 2020) represents the only other described permineralized Jurassic bryophyte fossil. It was described from a single gametophyte of an acrocarpous moss, and has affinities with the families Polytrichaceae or Timmiellaceae. Based on the preserved features, none of the morphotypes described here are closely comparable to *Heinrichsiella patagonica* (Bippus et al., 2019). However, Morphotype B shares with *H. patagonica* two key features: 1) unicostate

leaves with a strong and heterogeneous costa, and 2) bulging-mammillose lamina cells. These similarities indicate that Morphotype B is broadly similar to Timmiellaceae. However, the costal anatomy of *Heinrichsiella* and extant Timmiellaceae is otherwise different from that of Morphotype B. In distal portions of leaves, *Heinrichsiella* has a single stereid band, lacks abaxial epidermis and the leaf lamina is bistratose, whereas, Morphotype B has two stereid bands, adaxial and abaxial epidermis, and unistratose leaf lamina.

Livingstonites gabrielae Vera (2010) is known from several small permineralized shoots from the Early Cretaceous (Aptian) of Livingston Island (Vera, 2010). Based principally on the presence of single costate leaf with heterogeneous costa and unistratose lamina, *L. gabrielae* is similar to Morphotype B. However, in *L. gabrielae* the costa is composed by at least two layers of guide cells and one abaxial stereid band (Vera, 2010), which differs from the single layer of guide cells and two stereid bands present in Morphotype B.

Jamesrossia plicata Walker, Stockey, Rothwell, Atkinson, Smith et Iglesias (2024) from the Baculites Hill locality, Late Cretaceous, Santa Marta Formation (ca. 80 Ma) of Antarctica, correspond to an anatomically preserved moss gametophyte in a marine carbonate concretion (Walker et al., 2024). Like Morphotype B, *Jamesrossia plicata* has costate leaves, heterogeneous costa with large guide cells and the leaf lamina is unistratose. But differs from it in several features: Stem with central strand, leaf margins recurved, often bistratose, leaf lamina with two plications on either side of the costa, laminal cells lacking ornamentation, costa D-shaped in cross section, with small cells (probably sub-stereids) only abaxial to the guide cells (Walker et al., 2024).

Meantoina alopsoioides Bippus, Stockey, Rothwell et Tomescu (2017) is a permineralized polytrichaceous moss described from the Early Cretaceous (Valanginian) Apple Bay locality of Vancouver Island (British Columbia, Canada) (Stockey and Rothwell, 2006). As in *Livingstonites* species and Morphotype B, *M. alopsoioides* has unicostate leaves, with a heterogeneous costa and unistratose lamina (Bippus et al., 2017). This Early Cretaceous fossil differs from Morphotype B, principally, in the presence of photosynthetic lamellae. This taxonomically important feature, diagnostic of several distantly-related groups of acrocarpous mosses that live in high-light environments (e.g. Schiavone, 1993; Proctor, 2005), and it is not observed in Morphotype B.

Cynodontium luthii Bippus, Rothwell, et Stockey (2021) is a permineralized rhabdoweisiaceaceous moss described from the Late Cretaceous (Santonian/Campanian to Maastrichtian?) of northern Alaska (Bippus et al., 2021). Like Morphotype B, it has unicostate leaves with heterogeneous costa, with substereids, guide cells, and a central strand. However, *C. luthii* differs from Morphotype B in several features like a leaf blade keeled proximally and channeled distally, the leaf margins narrowly recurved proximally, occasionally bistratose and denticulate distally (Bippus et al., 2021).

Merceria augustica Smoot and Taylor (1986) is a Late Permian permineralized moss from Antarctica (Buckley Formation, Beacon Supergroup). This fossil is also comparable with Morphotype B based on the presence of single, strong and heterogeneous leaf costa. However, this silicified Permian moss differs from Morphotype B in the shape of laminal cells in transverse section, they are not bulging cells, and in some specimens there are parts of the lamina that are bistratose, unlike Morphotype B. Also, the heterogeneous costa of the Permian moss lacks stereid bands and guide cells, like those in the costa of Morphotype B.

Morphotype: C

Locality: Provincial Road 79 (coordinates 47°57'54.8"S 70°24'49.4"W), from La Aragonesa farm to El Frigorífico farm, Santa Cruz province, southern Argentina (Fig. 1).

Material: MPM - PB 16066.

Stratigraphic horizon: Massive gray to orange chert, uppermost part of the Bahía Laura Jurassic volcanic Complex (Fig. 1); upper Jurassic.

Diagnosis: Morphotype C can be recognized based on the following combination of features: 1) leaves with a single, narrow costa that is anatomically homogenous, 2) a leaf lamina composed of smooth, thin-

walled cells that are circular in cross section, and 3) stems that lack a central strand.

Description: This morphotype is known from three gametophyte shoots preserved in the same chert block (I, Fig. 4A; II, Fig. 4B; III, Fig. 4C; Appendix A). Each gametophyte is only known from a single thin section. Shoots are of small diameter (I: 1.3 mm; II: 0.77 mm; III: 1.8 mm) and unbranched. Stems are 234 to 295 μm in diameter and they are composed of isodiametric cells (18–25 μm in diameter) throughout, with cells becoming thicker-walled and smaller in diameter towards the stem surface (Fig. 4D). Oblique sections reveal that the outermost cells of the stem are longitudinally elongated (30 μm long) (Fig. 4E). Leaves are up to 1 mm wide, single costate, and their lamina are unistratose. The costa is narrow (73.7 μm wide $\times$ 44.5 μm thick), and plano-convex to biconvex in cross section (Fig. 4F). Costa anatomy is homogeneous

with thick walled cells (Fig. 4F). Laminal cells are smooth, thin-walled, and distinctly circular in cross section (12.8 μm in diameter) (Fig. 4G).

Comparisons between Morphotype C and extant bryophyte lineages: The absence of lignified vascular tissues indicates that Morphotype C represents a leafy bryophyte gametophyte. The presence of a costa discards affinities with leafy liverworts, whose leaves are exclusively ecostate (e.g. Schofield, 1985; Gradstein et al., 2001).

Individually, most of the gametophytic characters of Morphotype C are found in different groups of mosses (e.g. Gradstein et al., 2001; Ochrya et al., 2008; Frey and Stech, 2009). Broadly, similar morphologies are found in several families distributed across three moss subclasses: Funariidae (e.g., Funariaceae-Funariales) Dicranidae (e.g. Dicranaceae -Dicranales s.s., Rhabdoweisiaceae -Rhabdoweisiales, Grimmiaceae -Grimmiales and Pottiaceae -Pottiales) and Bryidae (e.g.,

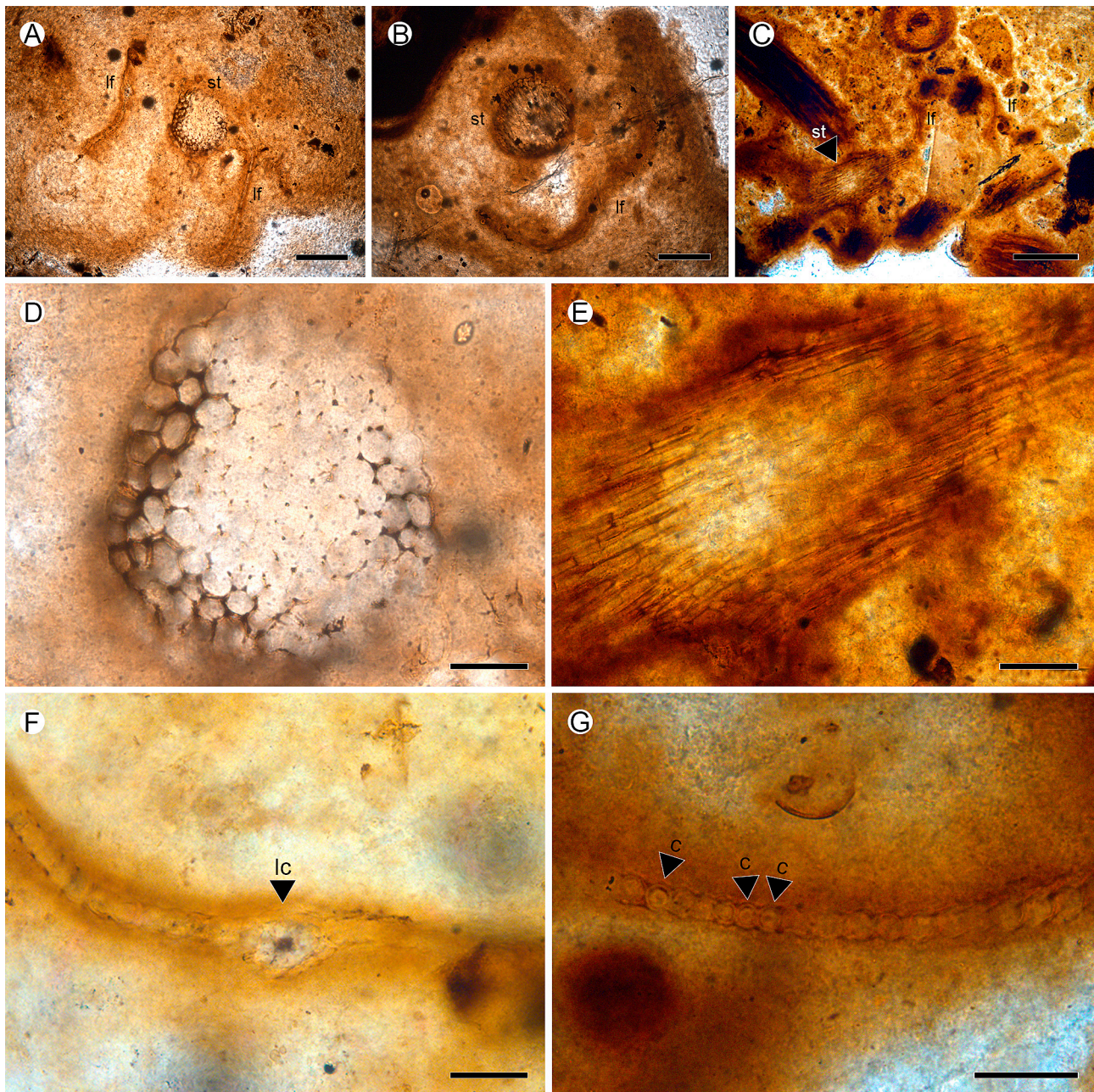


Fig. 4. Morphotype C from La Bajada locality. A–C. General aspect of the three shoots. D. Stem transverse section showing thicker outer cells and isodiametric thinner walled inner cells. E. Stem oblique-longitudinal section showing long rectangular cells. F. Leaf costa transverse section, showing the plane-convex section and homogeneous. G. Leaf lamina transverse section showing the smooth, thin-walled, and notably circular cells in transverse section. / Scale bars: A–B: 200 μm , C: 500 μm , D: 50 μm , E: 100 μm , F–G: 50 μm / lf: leaf; st: stem; lc: leaf costa; c: leaf laminal cells.

Bryaceae -Bryales, Orthotrichaceae -Orthotrichales and Amblystegiaceae -Hypnales).

Within the family Funariaceae some genera share several features with Morphotype C: Unicostate leaves, a unistratose lamina composed of smooth, and thin-walled cells that are circular in cross section (e.g., *Funaria*) (Ochyra et al., 2008; McIntosh, 2007). However, in this family the stems have a central strand and leaves have a notably different costal anatomy than that in the fossil (Crum and Anderson, 1955; McIntosh, 2007).

Several extant representatives of Subclass Dicranidae are morpho-anatomically similar to Morphotype C. Single costate leaves with a unistratose lamina composed of rounded smooth cells are found in some species of Dicranaceae, Rhabdoweisiaceae and Grimmiaceae. Many species of Dicranaceae and Grimmiaceae also have a narrow costa with anatomically undifferentiated cells also as in Morphotype C. These include the rhabdoweisiaceous genus *Kiaeria* (Kawai, 1968; Newmaster, 2007) and the grimmiaceous species *Grimmia hamulosa* (Muñoz and Pando, 2000; Hastings and Greven, 2007) and *Schistidium rivulare* (Fife, 2000). In contrast, other species of Dicranaceae generally have an anatomically heterogeneous costa (e.g., Ochyra et al., 2008; Suárez et al., 2013) except for some species of *Dicranella* that have a homogeneous costa (e.g. *D. rufescens*, *D. schreberiana*, *D. staphylina*; Müller and Lüth, 2021a, 2021b, 2021c). Within the family Pottiaceae, some extant taxa (e.g. *Gymnostomiella*) also share several features with the fossil (e.g. a single narrow costa, unistratose lamina, laminal cells rounded in section), but members of this family typically have papillose laminal cells and a more complex costal anatomy (Kawai, 1968; Zander and Eckel, 1993).

The fossil is also similar to some extant representatives of the subclass Bryidae (Ochyra et al., 2008; Frey and Stech, 2009; Goffinet and Shaw, 2009). Some taxa within the family Bryaceae have a single slender costa, and an unistratose lamina composed of oval-hexagonal, smooth, thin-walled cells that are circular in cross section (e.g. *Bryum microimbricatum* (Ochi, 1982), which is closely comparable to the morphology of Morphotype C. However, most bryaceous mosses have a stem with a central strand and a leaf costa with a strong stereid band (e.g. Kawai, 1968). The families Orthotrichaceae and Amblystegiaceae are also comparable with Morphotype C. The Orthotrichaceae share with Morphotype C a stem without a central strand, and leaves with a single costa, laminal cells that are mostly unistratose, and small and isodiametric cells in the upper lamina (e.g. *Orthotrichum affine*) (Lewinsky, 1993). However, all species of Orthotrichaceae differ from the fossil in other key features, including the presence of a strong costa, a lamina that generally develops multistratose areas, and laminal cells that vary from smooth to papillose (Ochyra et al., 2008; Lewinsky, 1984). Despite some similarities with Morphotype C, leaves of most members of Amblystegiaceae have a single homogenous costa and an unistratose lamina (Hédenas, 1994; Frey and Stech, 2009). Some species of *Drepanocladus* and *Warnstorfia* have smooth, thin-walled lamina cells that are circular in cross section (Ochyra and Matteri, 2001), like Morphotype C. However, members of these genera typically have a stem with a central strand, which is not observed in the fossil.

Comparison between Morphotype C and other anatomically preserved fossil bryophytes: *Tricarinnella crassiphylla* Savoretti, Bippus, Stockey, Rothwell et Tomescu (2018) also from Apple Bay, is characterized by the presence of a stem with a central conducting strand, a single homogeneous leaf costa and a lamina with bistratose portions and sinuous laminal cells (Savoretti et al., 2018). This fossil shares with Morphotype C a single, homogeneous leaf costa, but differs in most other features. For example, in Morphotype C, the stem lacks a central strand, laminal cells in sections are extremely rounded, and cell walls are thinner than in *Tricarinnella*. *Tricarinnella* also have leaves with a bistratose lamina basally and a unistratose lamina distally – such a combination of features is not found in any member of the La Bajada bryoflora, nor in any extant moss.

The bryoflora preserved at Apple Bay also includes an extinct family of Hypnanean mosses (Family Tricostaceae). This family is represented

by four species: *Tricosta plicata* (Shelton et al., 2015), *Krassiloviella limbelloides* (Shelton et al., 2015), *Tricosta priapiana* (Blanco-Moreno et al., 2023) and *Tricosta angeiophoros* (Valois et al., 2024). Morphotype C shares with these Early Cretaceous fossils several features including leaves with homogenous costa and oval-isodiametric laminal cells with smooth cell walls. However, the diagnostic feature of these Cretaceous fossils is that they have leaves that are tricostate (i.e., with three strong costae) and plicate (Shelton et al., 2015, 2016; Blanco-Moreno et al., 2023; Valois et al., 2024), which is not observed in any moss morphotype described here.

Morphotype: D

Locality: Provincial Road 79 (coordinates 47°57'54.8"S 70°24'49.4"W), from La Aragonesa farm to El Frigorífico farm, Santa Cruz province, southern Argentina (Fig. 1).

Material: MPM-PB 16071.

Stratigraphic horizon: Massive gray to orange chert, uppermost part of the Bahía Laura Jurassic volcanic Complex (Fig. 1); upper Jurassic.

Diagnosis: Morphotype D is defined based on the following combination of features: 1) Leaves concave and ecostate, 2) leaf lamina composed of smooth, thin-walled, bulging, rhomboidal cells, and 3) stems with a well-developed central strand. Among the bryophyte morphotypes present at La Bajada, Morphotype D is the only one that shows evidence of branching.

Description: This morphotype consists of one small shoot (1.3 × 0.5 mm) with excellent anatomical preservation (Fig. 5A, Appendix A). Three stem fragments are preserved. Based on their different disposition and plane of section, the two axes in cross section may represent branches (0.27 mm and 0.2 mm in diameter) diverging from the stem in the longitudinal section (0.43 mm in diameter). At least three leaves surround the stems (Fig. 5B). Leaves are concave and ecostate, with unistratose lamina of bulging, hexagonal-rhomboidal cells (Fig. 5C–D). Anatomically, the stems are characterized by an epidermal layer of thin-walled cells (Fig. 5E), 2–3 layers of thick walled cells (Fig. 5E) and a central strand of wavy, thin-walled cells (reminiscent of hydroids) (Fig. 5F). The outer layer of the stem has thin-walled cells, but it is not clear if it corresponds to a hyalodermis since these delicate cells are preserved in only one small portion of one of the stem sections (Fig. 5E).

Comparisons between Morphotype D and extant bryophyte lineages: Among the bryophyte morphotypes present at La Bajada, Morphotype D is the only one that shows evidence of branching. Morphotype D can be assigned to Bryophyta sensu stricto because it has a leafy shoot with complex stem anatomy, including a central strand formed by thin-walled cells (hydroids). Leafy liverworts have stems with varying degrees of anatomical complexity, but they never develop a central strand (Schofield, 1985; Gradstein et al., 2001).

Within mosses, Morphotype D has some similarities with the Dicranidae Pleurophascaceae (Order Pleurophascales) and with several families in subclass Bryidae: Bryaceae (Order Bryales), Hookeriaceae (Order Hookeriales), Hypnaceae and Plagiotheciaceae (Order Hypnales).

Morphotype D is comparable to the monotypic family Pleurophascaceae (Fife and Dalton, 2005). *Pleurophascum* shares with Morphotype D the presence of branched stems and ecostate leaves with oblong-hexagonal laminal cells (Fife and Dalton, 2005; Catcheside, 2012). However, *Pleurophascum* differs in several features with respect to the fossil. Specifically, *Pleurophascum* has strongly porose laminal cells unlike the fossil. *Pleurophascum* also has significant differences in stem anatomy with respect to Morphotype D, including a narrower central strand and weakly differentiated cortical cells (Fife, 2000; Frey and Stech, 2009; Catcheside, 2012).

Gametophytic features of bryalean mosses are highly variable (e.g., Gradstein et al., 2001; Ochyra et al., 2008; Goffinet and Shaw, 2009). Morpho-anatomical features of the leaves are variable even within families (e.g. Ochi, 1959, 1972, 1982; Ochyra et al., 2008). For example, in most Bryales the costa is single and strong, but there are some ecostate species that are comparable to Morphotype D. This fossil shares several

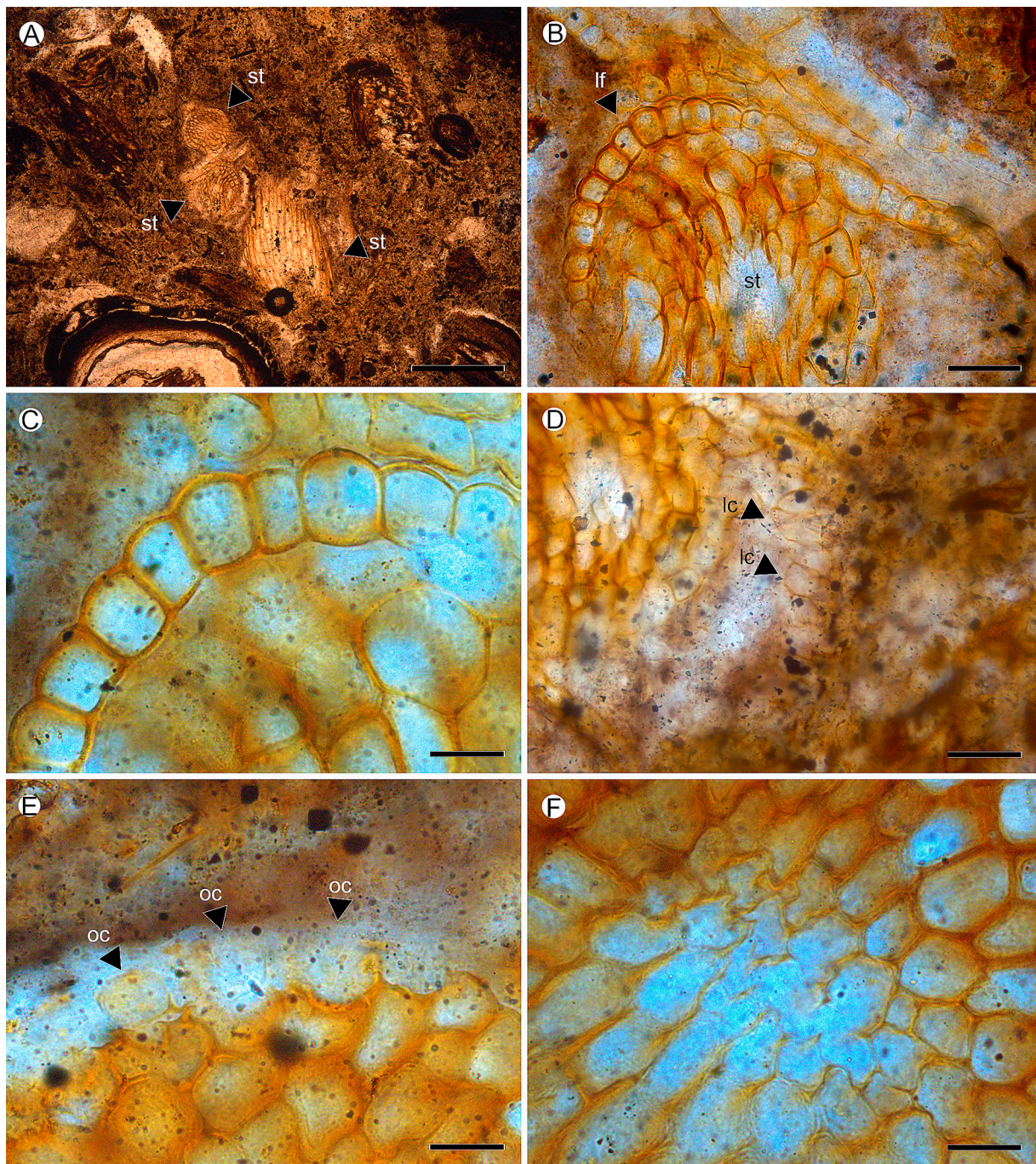


Fig. 5. Bryophyte morphotype D from La Bajada Locality. A. General aspect of Morphotype D shoot. B. Concave and ecostate leaves surrounding a stem. C. Unistratose lamina of bulging cells. D. Oblique paradermal section of hexagonal-rhomboidal laminal cells. E. Outer part of the stem section with an epidermal layer of thin-walled cells and 2–3 layers of thick-walled cells. F. Inner part of the stem section showing a central strand of wavy thin-walled, empty cells. / Scale bars: A: 500 µm, B: 50 µm, C: 20 µm, D: 50 µm, E: 20 µm, F: 20 µm. lf: leaf; st: stem; lc: lamina cells in a paradermal view; oc: stem outer thin-walled cells.

features with the genus *Bryum* (Bryaceae). *Bryum* is one of the largest and most polymorphous moss genera, comprising species with widely divergent morphologies (Ochi, 1982; Ochyra et al., 2008). Although most species of this genus present a well-developed costa, some varieties of the widespread species *Bryum argenteum* are an exception. In *B. argenteum* leaves are generally single costate. However, the costa is often very weak, and the extent of costal development is highly variable. The costa may be absent (e.g., *B. argenteum* var. *muticum*) or indistinct, or extend to near the mid-leaf, or sometimes be subpercurrent (Ochi, 1982; Ochyra et al., 2008). The former features together with the rhombic to rhomboidal shape of the laminal cells make these taxa comparable to

Morphotype D.

Among pleurocarpous mosses (Superorder Hypnanae), the family Hookeriaceae shares many features with Morphotype D. In this family, stems have a central strand, leaves are ecostate, leaf margins are entire and laminal cells are broadly oblong-hexagonal, oblong-rhomboidal, or short rectangular, with smooth cell walls (e.g., Eckel, 2010). This morphotype strongly resembles Hookeriaceae, but we cannot assign it to this group, as broadly similar combinations of characters are known in other groups of mosses.

A few genera in the Hypnales are morpho-anatomically comparable to Morphotype D. For instance, ecostate leaves with unistratose lamina

composed of smooth rhomboidal cells are also found in some species of *Platydictya* and *Plagiothecium* (Plagiotheciaceae -Buck and Goffinet, 2001; Tsubota et al., 2002, Goffinet et al., 2009). Furthermore, *Plagiothecium* also shares the presence of a central strand with Morphotype D. Despite these similarities, both genera also show conspicuous differences with Morphotype D. *Platydictya* differs in the presence of a narrow, or sometimes absent, central strand, whereas Morphotype D has a robust central strand. Additionally, in *Platydictya* rhizoids are borne in the leaf axils forming a tomentum and small and filiform pseudoparaphylla are borne on stems, neither of which are present (or at least not preserved) in Morphotype D (Ochyra et al., 2008; Ignatov and Spirina, 2012). In addition, leaves of *Plagiothecium* are variable. Many species of *Plagiothecium* bear some leaves with a forked costa although other leaves on the same plant may be ecostate (e.g., Wolski, 2020). Only a few cross sections of Morphotype D leaves are preserved, which precludes detailed understanding of leaf structure, including whether some leaves may be costate, as in *Plagiothecium*. Additional diagnostic features of *Plagiothecium* include the presence of intercalary rhizoids arising immediately below the leaf insertion or at the leaf tips, and of filiform axillary hairs (Buck and Ireland, 1989). However, none of these features are observed in the fossil.

Comparisons between Morphotype D and other anatomically preserved fossil bryophytes: Based on the absence of any previous record of Mesozoic ecostate moss preserved as a permineralization, the Morphotype D is not comparable with any of the fossils mentioned above.

4. Discussion

The combination of characters shown by each morphotype suggest affinities to two or more extant bryophyte orders or families. Bryophyte gametophytes generally have distinctive character combinations that allow assignment at fine taxonomic scales based on gametophytes alone even though sporophytes are generally considered to be more taxonomically informative (Flora of North America Editorial Committee, 2007, 2014). However, the incompletely preserved nature of La Bajada bryophyte gametophytes hinders more precise taxonomic placement. Therefore, the discovery of additional specimens from the geothermal paleoenvironments in Patagonia hold the potential to provide additional features able to further refine taxonomic assignments of the fossils characterized here. Moreover, the fossils described here are among the first anatomically preserved bryophytes from Jurassic strata and therefore significantly expand current knowledge of Jurassic bryophyte diversity.

4.1. Bryophytes of the Jurassic of Santa Cruz in a phylogenetic context

The morphotypes described here show a variable degree of certainty in terms of their taxonomic affinities, following recent phylogenetic topologies based on analyses of extant taxa using molecular datasets (Figs. 6, 7; Bechteler et al., 2023). The taxa here described do not represent the oldest representative of any lineage to which they may be assigned. However, it is still informative to define the most inclusive node to which they can be tentatively related.

The morphology recovered for morphotype A indicates affinities with the monophyletic class Marchantiidae and it is here considered as belonging to that node. Currently, the oldest known representative of Marchantiidae is *Hepaticites langii* Walton (Oostendorp, 1987), from the late Carboniferous of England. The affinities of morphotype A with Marchantiales and Neohodgsoniales suggest that it is a member of the clade that comprises these two orders and Sphaerocarpaceae (Fig. 6). As a class, Marchantiophyta represents an old lineage, the oldest unambiguous record is represented by *Metzgeriothallus sharonae* Hernick, Landing et Bartowski from the Middle Devonian Platekill Formation, New York, USA (Hernick et al., 2008).

On the other hand, the morphological information in morphotypes B, C and D do not support the unambiguous assignment to any particular

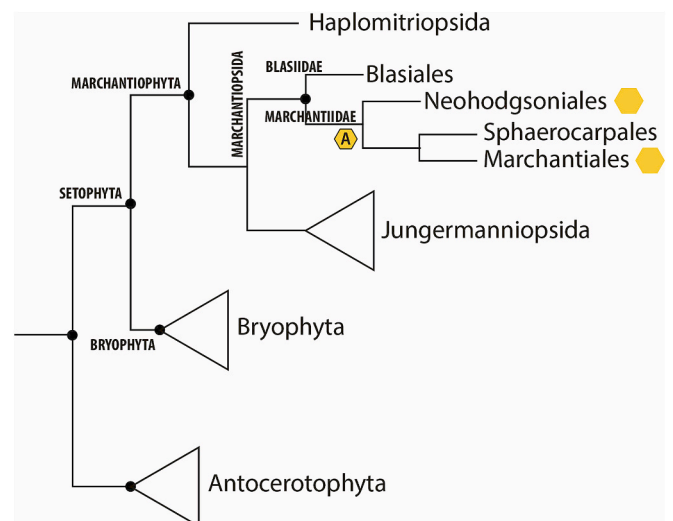


Fig. 6. Hypothetical systematic affinities of Morphotype A (yellow hexagons), based on morphological comparisons. Less inclusive node for Morphotype A is also indicated. Tree topology based on Marchantiophyta phylogeny modified from Bechteler et al., 2023. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Order within Bryophyta sensu stricto. The oldest fossils recognized as representatives of this ancient class are *Muscites plumatus* Thomas, from the Early Carboniferous (middle Mississippian - Visean) of England (Oostendorp, 1987; Tomescu et al., 2018) and three morphotypes from Ortelsdorf Formation (Carboniferous Early (middle Mississippian - Visean) of Germany (Hübers and Kerp, 2012). Mapping the hypothetical taxonomic affinities at the Order level for morphotypes B and C onto phylogenetic topologies based on nuclear gene data (Bechteler et al., 2023), both morphotypes can be related to the same node. The node include Funariales, to which both morphotypes are comparable, as well as a large clade in which Timmiales is sister to Dicranidae and Bryidae. In addition to Funariales, morphotype B may have affinities with Dicranidae, while morphotype C is morphologically similar to at least some Orders on both subclasses (Fig. 7). Finally, in the context of the same reference tree, the morphological configuration in morphotype D supports a more inclusive position, among the basal nodes of the Subclass Bryidae and Dicranidae (Fig. 7). The morphological characters preserved in this specimen have similarities to the basal-most lineage of this node, Bryales. However, affinities with the derived pleurocarp order Hypnales, and with the Dicranidae Pleurophascales cannot be discarded.

When the species *Heinrichiella patagonica* is considered in the context of the same topology, it supports a less inclusive node since its morphology suggests affinities to the family Polytrichaceae or Timmiellaceae, the former of which occupies a more basal position within Bryophyta than any of the other Deseado Massif bryophytes (Fig. 7).

5. Final remarks

Even though most of the fossils described in this manuscript are only known from a small number of specimens, and their gross morphology could not be completely reconstructed, they reveal that the Jurassic geothermal localities in Patagonia preserve representatives of multiple bryophyte lineages. This work is the first step towards documenting the anatomically-preserved Jurassic bryophyte flora. The continuous discovery of new localities representing different parts of this Jurassic system, together with the growing number of collected and sectioned samples, will certainly allow for the description of new bryophytes, and for a better circumscription of the morphotypes here described, based on additional structures.

Furthermore, as the first permineralized pre-Cretaceous flora with

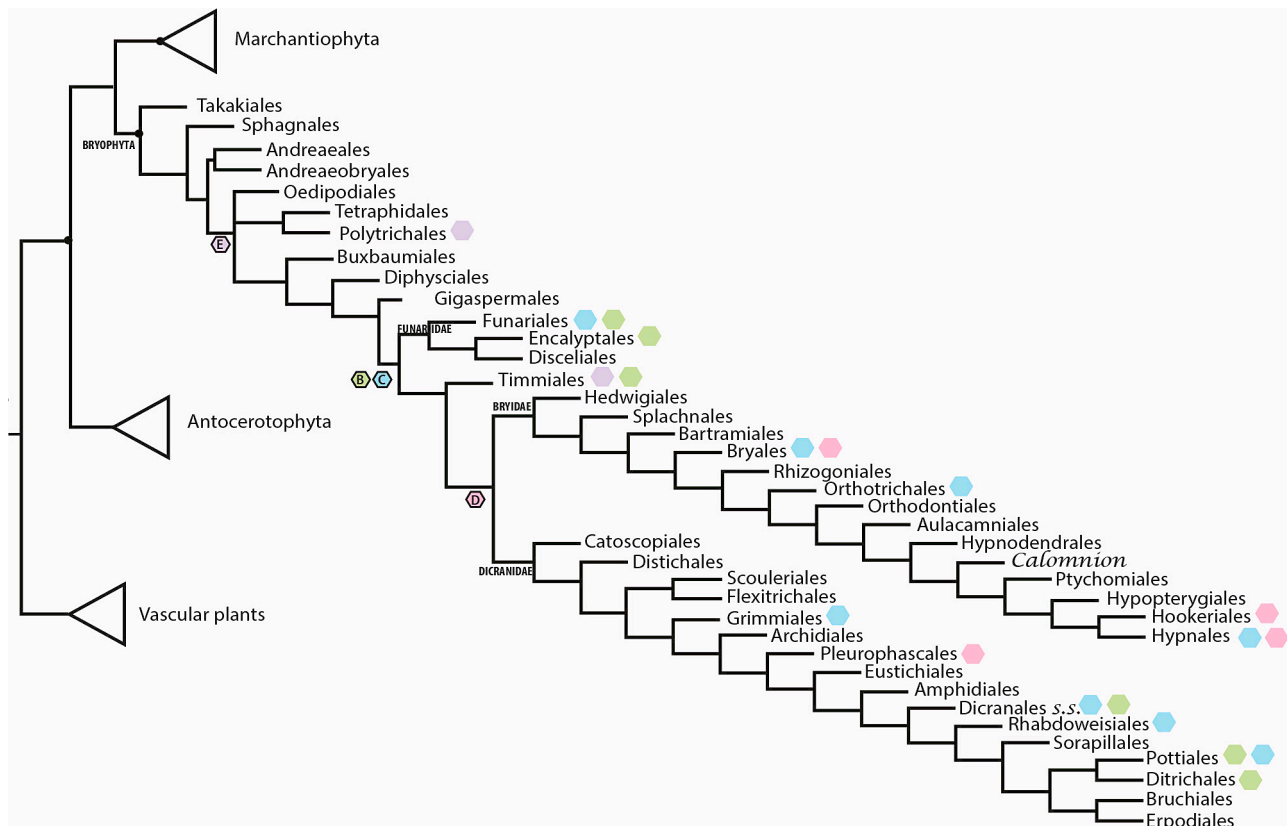


Fig. 7. Hypothetical systematic affinities of morphotypes B (green hexagons), C (light blue hexagons), and D (pink hexagons), based on morphological comparisons. Letter E (violet hexagons) indicates the phylogenetic position of *Heinrichsiella patagonica* from the Jurassic period. Less inclusive nodes for each morphotype are also indicated. Tree topology based on Bryophyte phylogeny, modified from Bechteler et al., 2023. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

multiple bryophytes, La Bajada flora provides the first high resolution snapshot of Jurassic bryophyte diversity. Accordingly, it deeply enriches our understanding of the mode and tempo of Mesozoic bryophyte evolution by extending our knowledge of patterns in bryophyte evolution deeper in time. Several of the permineralized bryophytes from the Deseado Massif have novel combinations of characters or character combinations that are found in multiple, distantly related families of bryophytes, suggesting that these plants may pre-date the origin of most extant families. The oldest mosses unequivocally assignable to extant families come from Early Cretaceous deposits that are only ~15 million years younger, and have mosaics of features found in extant genera (Bippus et al., 2017; Savoretti et al., 2018; Bomfleur et al., 2023) while the oldest unequivocal reports of extant bryophyte genera come from the Late Cretaceous (Konopka et al., 1998; Bippus et al., 2021). Therefore, the La Bajada bryophytes provide additional data that positions the Jurassic as a critical period in the evolution of extant bryophyte families and genera.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2025.105321>.

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