Extending the fossil record of Polytrichaceae: Early Cretaceous *Meantoinea alophosioides* gen. et sp. nov., permineralized gametophytes with gemma cups from Vancouver Island[1]

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PREMISE OF THE STUDY: Diverse in modern ecosystems, mosses are dramatically underrepresented in the fossil record. Furthermore, most pre-Cenozoic mosses are known only from compression fossils, lacking detailed anatomical information. When preserved, anatomy vastly improves resolution in the systematic placement of fossils. Lower Cretaceous deposits at Apple Bay (Vancouver Island, British Columbia, Canada) contain a diverse anatomically preserved flora that includes numerous bryophytes, many of which have yet to be characterized. Among them is a polytrichaceous moss that is described here.

METHODS: Fossil moss gametophytes preserved in four carbonate concretions were studied in serial sections prepared using the cellulose acetate peel technique.

KEY RESULTS: We describe *Meantoinea alophosioides* gen. et sp. nov., a polytrichaceous moss with terminal gemma cups containing stalked, lenticular gemmae. Leaves with characteristic costal anatomy, differentiated into sheathing base and free lamina and bearing photosynthetic lamellae, along with a conducting strand in the stem, place *Meantoinea* in family Polytrichaceae. The bistratose leaf lamina with an adaxial layer of mamillose cells, short photosynthetic lamellae restricted to the costa, and presence of gemma cups indicate affinities with basal members of the Polytrichaceae, such as *Lyellia*, *Bartramiopsis*, and *Alophosia*.

CONCLUSIONS: *Meantoinea alophosioides* enriches the documented moss diversity of an already-diverse Early Cretaceous plant fossil assemblage. This is the third moss described from the Apple Bay plant fossil assemblage and represents the first occurrence of gemma cups in a fossil moss. It is also the oldest unequivocal record of Polytrichaceae, providing a hard minimum age for the group of 136 million years.

KEY WORDS   anatomy; Bryophyta; Cretaceous; fossil; gametophyte; gemmae; lamellae; moss; permineralized; Polytrichaceae

The Polytrichaceae, sole family of the class Polytrichopsida, is a diverse and evolutionarily distinct group of mosses characterized by a high level of sporophyte and gametophyte complexity (Smith, 1971; Schofield, 1985; Smith Merrill, 2007). In most cases,

Polytrichaceous moss gametophytes are easily recognizable by their complex leaves, which typically bear adaxial photosynthetic lamellae and have sophisticated conducting tissues (Smith, 1971; Hébant, 1977). Polytrichaceous sporophytes are equally distinctive, since most species have many nonhygroscopic, nematodontous, peristome teeth, which are considered nonhomologous to those of other moss lineages (Smith Merrill, 2007; Bell and Hyvönen, 2008). While these features are generally conserved within the family, polytrichaceous mosses have a broad range of growth habits, including the largest and most anatomically complex moss gametophytes (e.g., *Dawsonia superba* Greville; Zanten, 1973), as well as mosses with extremely small ephemeral shoots and long-lived protonemata (e.g., *Pogonatum camusii* Touw; Hyvönen, 1989).

The family Polytrichaceae has no close living relatives and, therefore, it is not clear how distinguishing characters, e.g., photosynthetic lamellae, distinctive peristome, and complex conducting tissues, evolved (Renzaglia et al., 2007; Bell and Hyvonen, 2008; Chang and Graham, 2014). Given this absence of close living relatives, fossils are crucial for understanding the early evolution of the Polytrichaceae. Fortunately, compared with other mosses, the Polytrichaceae have a rich Cenozoic fossil record (i.e., younger than 66 Ma), with 10 species described from Europe, North America, and Asia (Göppert, 1853; Knowlton, 1926; Yasui, 1928; Frahm, 2004, 2010). Unfortunately, very few moss fossils reported from older sediments are available to throw light on earlier stages in the evolution of this basal moss lineage.

Here we describe an anatomically preserved polytrichaceous moss of Early Cretaceous age (Valanginian, ca. 136 Ma), based on five permineralized gametophyte shoots from the Apple Bay locality on Vancouver Island (British Columbia, Canada). This moss is described as a new genus and species, characterized by terminal gemma cups bearing lenticular gemmae, leaves with low photosynthetic lamellae restricted to the costa, and a bistratose lamina with an adaxial layer of mamillose cells. This is one of the most completely known pre-Cenozoic fossil mosses to date and represents the oldest unequivocal record of the Polytrichaceae and the first report of gemma cups in a fossil moss. This discovery offers a crucial look at pre-Cenozoic polytrichaceous moss diversity, which is necessary for understanding evolution in this distinctive and diverse bryophyte lineage.

MATERIALS AND METHODS

The focus of this study is the most completely known unicostate moss gametophyte from Apple Bay. Five gametophytes of this moss are preserved by cellular permineralization in four carbonate concretions, as part of an allochthonous fossil assemblage deposited in nearshore marine sediments (e.g., Stockey and Rothwell, 2009). The concretions were collected from sandstone (greywacke) beds exposed on the northern shore of Apple Bay, Quatsino Sound, on the west side of Vancouver Island, British Columbia, Canada (50°36′21″N, 127°39′25″W; UTM 9U WG 951068) (Stockey and Rothwell, 2009). The concretion-bearing layers are regarded as Longarm Formation equivalents and have been dated by oxygen isotope analyses to the Valanginian (Early Cretaceous, ca. 136 Ma) (Stockey et al., 2006; D. Gröcke, Durham University, UK, personal communication).

This diverse Early Cretaceous flora includes lycophytes, equisetophytes, at least 10 families of ferns (Smith et al., 2003; Hernandez-Castillo et al., 2006; Little et al., 2006a, b; Rothwell and Stockey, 2006; Stockey et al., 2006; Vavrek et al., 2006; Rothwell et al., 2014) and diverse gymnosperms (Stockey and Wiebe, 2008; Stockey and Rothwell, 2009; Klymiuk and Stockey, 2012; Rothwell and Stockey, 2013, 2016; Rothwell et al., 2014; Atkinson et al., 2014a, b; Ray et al., 2014; Klymiuk et al., 2015), as well as fungi (Smith et al., 2004; Bronson et al., 2013) and a lichen whose thallus shows modern heteromerous organization (Matsunaga et al., 2013). The Apple Bay flora is also emerging as the most diverse pre-Cenozoic assemblage of fossil bryophytes (Shelton et al., 2015; Tomescu, 2016), with liverworts and many distinct moss morphotypes. Recently, a new family of tricostate mosses was described and subsequently expanded based on permineralized material from Apple Bay (Shelton

et al., 2015, 2016). These mosses, including *Tricosta plicata* Shelton, Stockey, Rothwell, et Tomescu (as the most completely known moss gametophyte in the fossil record) and *Krassiloviella limbelloides*, also provide the earliest hard evidence for hypnanaean pleurocarpous mosses.

Fossil-containing concretions were sliced into slabs and sectioned using the cellulose acetate peel technique (Joy et al., 1956). Slides were prepared using Eukitt, a xylene-soluble mounting medium (O. Kindler GmbH, Freiburg, Germany). Micrographs were taken using a Nikon Coolpix E8800 digital camera on a Nikon Eclipse E400 compound microscope. Images were processed using Photoshop (Adobe, San Jose, California, USA). All specimens and preparations are housed in the University of Alberta Paleobotanical Collections (UAPC-ALTA), Edmonton, Alberta, Canada.

SYSTEMATICS

Class—Polytrichopsida Doweld.

Order—Polytrichales M. Fleisch.

Family—Polytrichaceae Schwägrichen.

Genus—*Meantoinea* Bippus, Stockey, Rothwell et Tomescu, gen. nov.

Generic diagnosis—Gametophytes unbranched. Leaves strongly costate with distinct sheathing base and free blade; costa with stereids and central arc of deuters. Photosynthetic lamellae restricted to costa of leaf blade. Leaf blade with bistratose lamina; adaxial cells mamillose, abaxial cells bulging. Leaf margins bearing unicellular teeth. Terminal gemma cups composed of densely packed undifferentiated leaves.

Etymology—*Meantoinea* is named in recognition of Marie E. Antoine's (Humboldt State University) key contribution to the bryological training of many students of the Apple Bay bryoflora.

Type species—*Meantoinea alophosioides* Bippus, Stockey, Rothwell et Tomescu, sp. nov.

Specific diagnosis—Gametophyte shoots unbranched, at least 4 mm tall. Stem diameter ca. 0.3 mm. Stem cross section with epidermis of small cells; central strand ca. 0.1 mm thick. Leaves densely packed along stem, 2/5 phyllotaxis. Leaves at least 2.64 mm long. Leaf base with unistratose lamina, 540–960 μm wide, clasping stem along ca. 0.6 mm. Leaf blade much narrower than sheathing base, ca. 150–500 μm wide; linear, with bistratose lamina. Costa strong, abaxially convex, up to 290 μm wide in leaf base, up to 153 μm wide in leaf blade. Costal anatomy complex; deuters forming central arc. Thick stereid band abaxial to deuters; abaxial epidermis with isodiametric cells; smaller conducting parenchyma adaxial to deuters; overlain by adaxial layer of intermixed parenchyma and stereids. Adaxial cells of bistratose leaf blade lamina thick-walled, mamillose; abaxial cells of lamina smaller, bulging in distal leaf region. Leaf margins with thick-walled unicellular teeth. Adaxial lamellae in 4–10 rows restricted to costa of leaf blade. Lamellae 2–3 cells (31–40 μm) tall with mamillose marginal cells and smaller isodiametric regular cells. Terminal gemma cups of densely packed undifferentiated leaves, containing ca. 6 stalked gemmae. Gemma
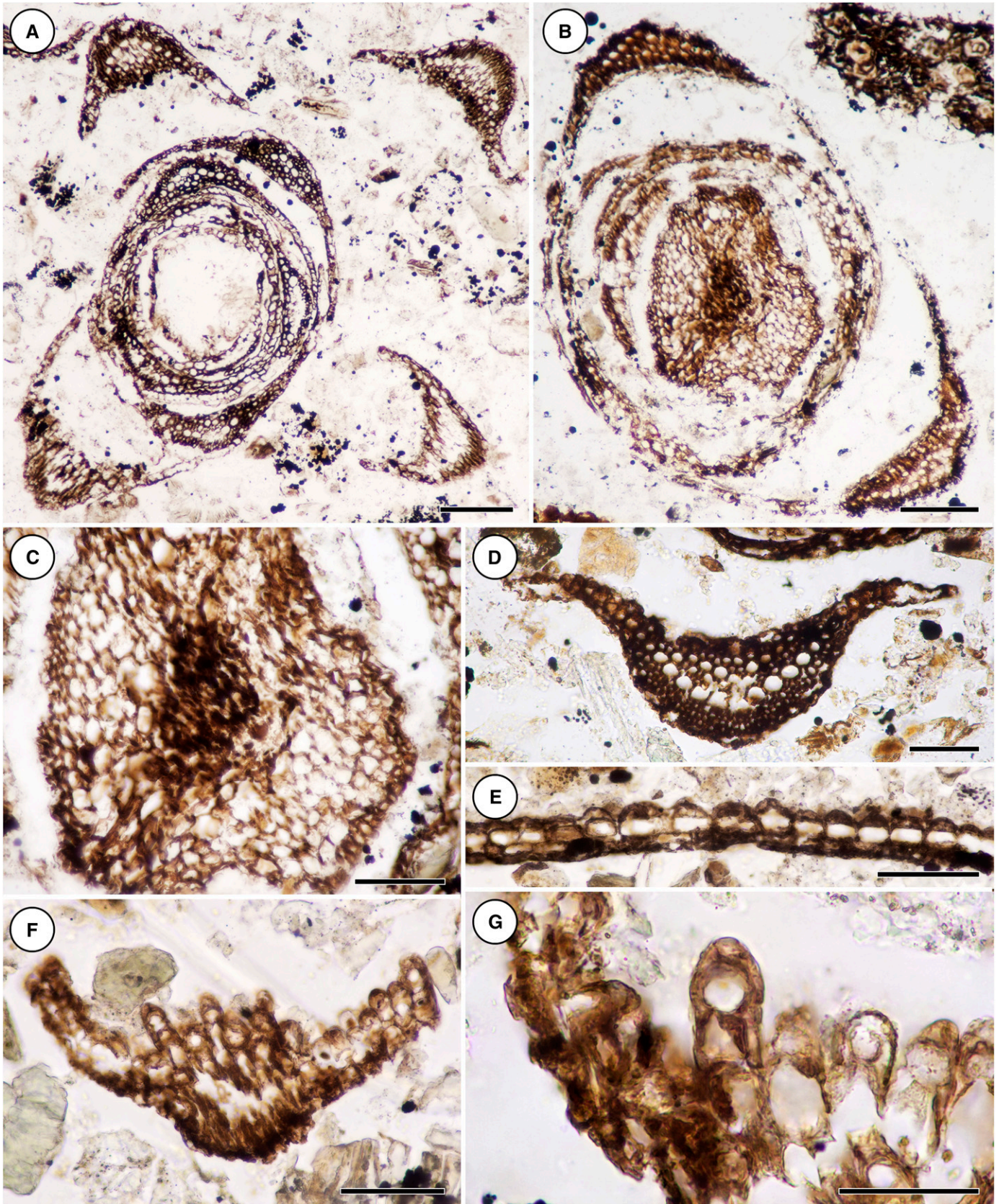
cups ca. 2.6 mm wide, 1.2 mm deep. Gemmae lenticular, ca. 100 × 100 × 50 μm; gemma stalk short, rhizoid-like.

Etymology—The specific epithet, *alophosioides*, refers to the close similarity between this species and *Alophosia azorica* (Renauld et Cardot) Cardot.

Holotype hic designatus—Gemmiferous gametophyte shoot in rock slab UAPC-ALTA P15393 B (slides B bot series a).

Paratypes—UAPC-ALTA P13158 Cbot; P15800 Cbot.

Locality—Apple Bay, Quatsino Sound, northern Vancouver Island, British Columbia, Canada (50°36′21″N, 127°39′25″W; UTM 9U WG 951068).

Stratigraphic position and age—Longarm Formation equivalent; Valanginian, ca. 136 Ma (Early Cretaceous).

DESCRIPTION

Habit and stem anatomy—Gametophyte shoots, traced for up to 4 mm of length have stems 192–346 μm in diameter (mean = 272.9 μm; *N* = 9). None of the specimens exhibits branching. Anatomically, stems are composed of three distinct layers (Fig. 1B, 1C): an outermost epidermal layer, one to several cells thick, consisting of small isodiametric cells 6–10 μm in diameter (mean = 7.5 μm; *N* = 12); a cortex composed of larger isodiametric cells 10–24 μm in diameter (mean = 15.4 μm; *N* = 10); and a central conducting strand ca. 100 μm in diameter, preserved in only one of the specimens and consisting of narrow and taphonomically compressed cells (Fig. 1B, 1C).

Leaf morphology and anatomy—The shoots have 2/5 phyllotaxis (Fig. 3). In the apical portion of a shoot that terminates in a gemma cup (Figs. 3, 4), leaves at successive nodes are spaced 60-90 μm apart. The leaves have a broad base that sheathes the stem and a much narrower blade that is adaxially concave and diverges at a wide angle (Figs. 1A, 1F, 2C–2G). The transition from leaf base to leaf blade, observed in serial transverse sections, is associated with a sharp decrease in width (Figs. 1A, 2C–2G). Leaf tips are sometimes recurved and are incompletely preserved (Figs. 2E–2G, 6). Leaves have a strong costa that runs the entire preserved length of leaves and comprises 25–30% of leaf width. The costa protrudes abaxially and is broader and thinner in the leaf base (Fig. 1D), becoming narrower and thicker, with a semicircular profile distally (Figs. 1F, 2C–2G). The leaf blades bear adaxial photosynthetic lamellae

covering the entire width of the costa (Figs. 1F, 1G, 2C–2G, 2I) and the entire preserved length of the leaf blade.

Leaf bases are 540–960 μm wide (mean = 694.3 μm; *N* = 17), sheathing the stem for ca. 0.6 mm before the leaf blade curves away from the stem. The linear blade, at least 2 mm long and 75% of overall leaf length, is much narrower than the base, 142–482 μm (mean = 308 μm; *N* = 21) (Fig. 6). Leaf length was reconstructed based on three series of sections that represent partial lengths of three distinct leaves; the three leaves have closely similar sizes (in cross section), and the three series are partially overlapping longitudinally. Leaf bases have a broad unistratose lamina consisting of square-isodiametric cells 7.2–15.6 μm (mean = 10.7 μm; *N* = 9), with the marginal cells significantly smaller than other laminal cells. Leaf blades have a much narrower bistratose lamina. The adaxial cells of the lamina are thick-walled, mamillose, and 8.4–13.0 μm wide × 12.0–16.8 μm tall × 12.0–16.8 μm long. The abaxial cells of the lamina are isodiametric in cross section, with an abaxial bulge, 7.2–12.0 μm wide × 8.4–13.2 μm tall × 14.4–15.6 μm long; in the transition zone between leaf base and leaf blade, cells of the abaxial lamina lack an abaxial bulge and are not as tall as those further up the blade. Leaf margins bear thick-walled unicellular teeth 27 μm long (mean = 24.6; *N* = 2) × 10.8 μm wide.

The costa is 120–288 μm wide (mean = 185.5 μm; *N* = 23) and 40.8–92.4 μm thick (mean = 62.9 μm; *N* = 14) in the sheathing leaf bases. In the leaf blade, the costa is up to 153 μm wide and 90–104 μm thick basally, tapering toward the leaf tip. In cross section, the costa shows several distinct layers. The central region is occupied by an arc of large (9.6–16.8 μm; mean = 13.5 μm; *N* = 8), elongated, thick-walled deuter cells with circular cross-sectional outline, comparable to those of extant Polytrichaceae (e.g., Smith, 1971; Hébant, 1977); "deuter" is a term used for specialized cells of the leaf costa that are thought to conduct photosynthates (see Hébant, 1977). Abaxial to the deuters, is a 3–5 cell thick zone of small-diameter (3.6–6 μm; mean = 4.1 μm; *N* = 13), thick-walled stereids. Abaxial to this band of stereids, the epidermis consists of small, 6.0–7.2 μm (mean = 6.6 μm; *N* = 8) diameter cells; the arrangement of these cells gives the costa an abaxially grooved surface (Figs. 1F, 2G). Adaxial to the deuters, is a layer of smaller-diameter circular cells (8.4–12.0 μm; mean = 10.3 μm; *N* = 10) comparable to the conducting parenchyma described in the costa of some polytrichaceous mosses (Hébant, 1977; Scheirer, 1983). Primarily adaxial to, but also intergrading with, the conducting parenchyma is a second thin band of stereids similar to the abaxial ones.

The leaf blades bear for their entire preserved length 4–10 photosynthetic lamellae restricted to the adaxial surface of the costa (Figs. 1F, 1G, 2C–2G, 2I, 6). The lamellae are 2–3 cells tall (ca. 30–40 μm overall height; mean = 36.1 μm; *N* = 8) and consist of small, isodiametric cells (8.4–14.4 μm; mean = 11.8 μm; *N* = 7). The mar-

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FIGURE 1 Stem and leaf anatomy of *Meantoinea alophosioides* gen. et sp. nov. (A) Cross section of shoot showing several sheathing leaf bases tightly wrapped around stem and four leaves sectioned in transitional region between leaf base and leaf blade; scale bar = 100; P15393 Bbot #7b. (B) Cross section of shoot with stem anatomy fully preserved; scale bar = 100 μm; P13158 Cbot #6c. (C) Detail of stem anatomy in B showing peripheral layer of small-diameter cells, cortex with larger cells, and central conducting strand; scale bar = 50 μm; P13158 Cbot #6c. (D) Cross section of costa in leaf base, showing deuters (layer of large cells), putative conducting parenchyma (layer of smaller cells adaxial to deuters), and small stereids on adaxial and abaxial side of costa; scale bar = 50 μm; P15393 Bbot #13b. (E) Longitudinal section of lamina close to base of leaf blade, showing bistratose lamina with adaxial mamillose cells; scale bar = 50 μm; P15393 Bbot #1b. (F) Cross section of leaf blade with several photosynthetic lamellae adaxial on costa; scale bar = 50 μm; P15393 Bbot #10b. (G) Detail of photosynthetic lamellae in Fig 2D; note mamillose, distalmost cell of lamella; Scale bar = 25 μm; P15393 Bbot #16b.
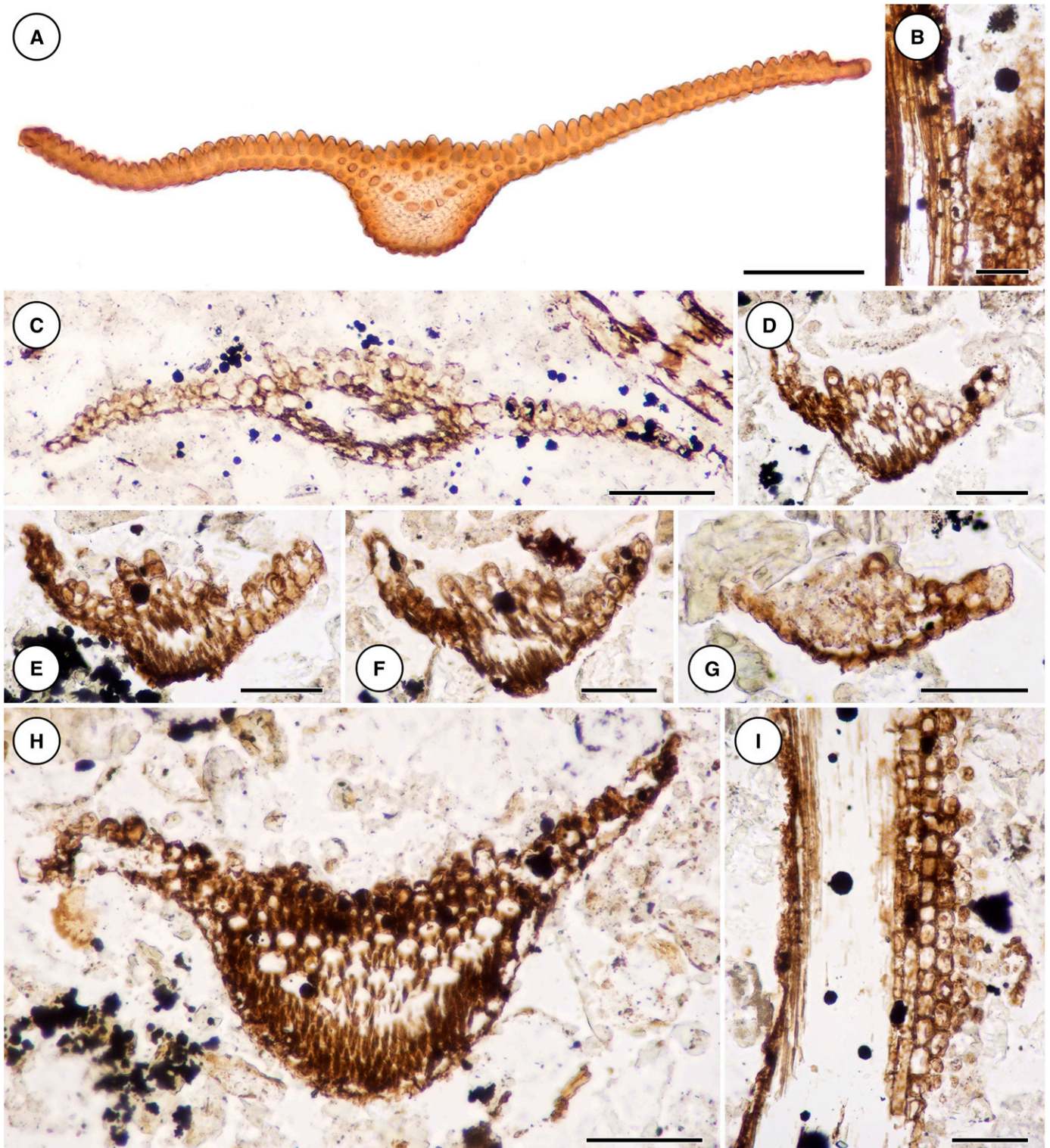
FIGURE 2 Leaf anatomy and morphology of *Meantoinea alophosioides* gen. et. sp. nov. and comparison with *Alophosia azorica*. (A) Cross section of basal portion of *Alophosia azorica* leaf blade, showing similar anatomy to *M. alophosiodes* (costa anatomy and bistratose lamina with adaxial mamillose cells); photo courtesy of J. Hyvönen and N. E. Bell; scale bar = 100 μm. (B) Paradermal section of *M. alophosioides* leaf blade with unicellular teeth at margin; scale bar = 50 μm; P15393 Bbot #2b. (C) Cross section of basal portion of *M. alophosioides* leaf blade, showing bistratose lamina and adaxial photosynthetic lamellae on costa; note similarities with 2A; scale bar = 100 μm; P15800 Cbot #4c. (D) Cross section of apical portion of *M. alophosioides* leaf blade, showing prominent adaxial photosynthetic lamellae with mamillose, distalmost cells; scale bar = 50 μm; P15393 Bbot #16b. (E–G) Cross sections of same *M. alophosioides* leaf blade illustrating morphological change along proximal-distal axis; note persistent costa, reduced lamina and

ginal cells of lamellae are thick-walled and mamillose in a similar way to the adaxial lamina cells. These marginal cells are 12–14.4 μm wide (mean = 13.4 μm; *N* = 7) and 15.6–19.2 (mean = 17.3 μm; *N* = 7) μm tall.

Asexual reproductive structures—One of the four gametophyte shoots terminates in a gemma cup formed by densely packed leaves, similar to the gemma cups of *Tetraphis pellucida* Hedwig (Crum, 2001) and *Alophosia azorica* (Renault and Cardot) Cardot (Smith, 1971). The cup is 2.6 mm in diameter and 1.2 mm deep and contains six laterally flattened gemmae (Fig. 4A, 4C, 5A). The gemmae measure ca. $100 \times 100 \times 50$ μm and are borne on short stalks ca. 8.5 μm in diameter. In cross sections of the cup, each gemma displays up to 10 relatively large, thin-walled isodiametric cells (13.2–24 μm; mean = 18; *N* = 10). These lenticular gemmae have a unistratose margin and are closely similar to those of *Tetraphis pellucida* (Fig. 4D, 5B) and *Alophosia azorica* (Crum, 2001; Smith, 1971).

DISCUSSION

***Taxonomic placement of* Meantoinea alophosioides *gen. et sp. nov.*—**A diagnostic suite of characters unequivocally place *Meantoinea* in the moss family Polytrichaceae. First, the leaves have a complex costal anatomy with deuters, stereids, and conducting parenchyma typical of polytrichaceous mosses (Smith, 1971; Hébant, 1977; Scheirer, 1983). Second, the leaves are differentiated into a broad sheathing leaf base with a unistratose lamina and a narrower leaf blade, a morphology found in many polytrichaceous mosses (Smith, 1971; Schofield, 1985). Third, the leaf blade has a bistratose lamina with an adaxial layer of mamillose cells, a feature of basal Polytrichaceae [e.g., *Alophosia* Cardot, *Lyellia* Brown, and *Bartramiopsis* (James) Kindberg; Smith, 1971; Bell and Hyvonen, 2010]. Fourth, the stem has a robust conducting strand, which is found in almost all polytrichaceous mosses (Smith, 1971). Fifth, the leaves of *M. alophosioides* bear low adaxial, unbranched photosynthetic lamellae with mamillose marginal cells. Finally, *M. alophosioides* produces stalked lenticular gemmae that are extremely similar to those produced by the polytrichaceous moss *Alophosia azorica* (Smith, 1971). Several moss lineages combine some features from this list, but the Polytrichaceae is the only group in which all the above features co-occur.

A few genera in the Pottiaceae (*Pterygoneurum* Juratzka, *Aloina* Kindberg, *Aloinella* Cardot, and *Crossidium* Juratzka) have adaxial outgrowths on leaves, a central strand in the stem, and complex costal anatomy (Delgadillo, 1975; Zhao et al., 2008; Zander, 2007). However, only in *Pterygoneurum* are the adaxial outgrowths organized into longitudinal files forming lamellae; adaxial leaf outgrowths in the other three pottiaceous genera are just irregularly arranged filaments (Zander, 2007; Zhao et al., 2008). Species of *Pterygoneurum* differ from *Meantoinea* in several characters: taller lamellae (ca. 12 cells tall), occasional branching of stems, absence of mamillose marginal cells, unistratose lamina, leaves not differentiated

into a broad sheathing base and narrow blade, and absence of gemma cups. *Aligrimmia peruviana* Williams (Grimmiaceae) also has complex costal anatomy, adaxial photosynthetic lamellae, and a central strand, but is significantly different from *Meantoinea* in its taller lamellae (6–7 cells tall) with undifferentiated marginal cells, a unistratose lamina, and lack of gemma cups (Murray, 1984).

Justification for a new genus—Compared with extant members of the Polytrichaceae, *Meantoinea* is most similar to three genera: *Alophosia*, *Lyellia*, and *Bartramiopsis* (Table 1). In addition to polytrichaceous characters more broadly shared within the family, *Meantoinea* shares with these three genera the bistratose lamina with an adaxial layer of mamillose cells and leaves differentiated into a broad sheathing base and a narrow blade, as well as comparable costal anatomy. Despite these similarities, the gametophytes of *Meantoinea* are different from each of the three genera in a number of ways (Table 1). First, *Alophosia*, *Lyellia*, and *Bartramiopsis* all have multicellular teeth at their leaf margins, whereas *Meantoinea* has unicellular teeth. Second, in contrast to *Meantoinea*, *Bartramiopsis* and *Lyellia* have taller lamellae with round marginal cells and do not produce gemma cups. Third, unlike *Meantoinea*, *Lyellia* produces double teeth and low lamellae abaxially on leaves (Ivanova and Ignatov, 2007). Fourth, although *Alophosia* produces gemmae in gemma cups quite similar to those of *Meantoinea* and has costal anatomy closely similar to the latter, that genus differs significantly from the fossil by completely lacking photosynthetic lamellae.

Meantoinea is also substantially different from both of the known genera of extinct Polytrichaceae: *Polytrichites* Britton and *Eopolytrichum* Konopka, Herendeen, Smith Merrill et Crane (Mägdefrau, 1957; Konopka et al., 1997; Frahm, 1999, 2010). *Eopolytrichum antiquum* Konopka, Herendeen, Smith Merrill et Crane is based on charcoalified sporophyte capsules from the Campanian (Late Cretaceous) of Georgia, United States, but several charcoalified gametophytes with polytrichaceous features have been described in association (but not physical connection) with the type material and may represent the same species (Konopka et al., 1997). *Meantoinea* is notably different from the gametophytes associated with *E. antiquum* in two ways. First, *Eopolytrichum* bears lamellae on both the costa and lamina of the leaf blade, whereas *Meantoinea* bears lamellae only on the costa. Second, *Meantoinea* has a bistratose leaf blade lamina with mamillose cells, whereas *Eopolytrichum* has a unistratose lamina.

The genus *Polytrichites* is a form genus for polytrichaceous fossils that do not preserve enough diagnostic information to be placed in any of the other known genera (Frahm, 2010). This genus includes two species known from Eocene Baltic amber (Frahm, 2010), one species known from compressions in the Miocene of Washington, United States (Knowlton, 1926), and an anatomically preserved shoot fragment from the Upper Miocene of Japan (Yasui, 1928; Yamada et al., 2015). Given the disparity between the level of preservation of *Meantoinea*, which provides tremendous detail on the morphology and anatomy of this moss, and the much less completely characterized fossils included in genus

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lamellae close to leaf tip (G); scale bars = 50 μm; P15393 Bbot #12b (E), #15b (F), #20b (G). (H) Cross section of *M. alophosioides* leaf at transition from sheathing leaf base to leaf blade; note costal anatomy with deuters (large), conducting parenchyma, and two bands of stereids; scale bar = 100; P15393 Bbot #7b. (I) Paradermal section of leaf blade; note parallel vertical rows of adaxial mamillose lamina cells (round, at right), abaxial lamina cells (rectangular, at right); cells (deuters) in middle of the costa (center) incompletely preserved; scale bar = 50 μm; P15393 Bbot #1b.

Polytrichites, the latter is not an appropriate placement for the Apple Bay moss.

The genera of living Polytrichaceae are differentiated primarily based on sporophyte characters (Smith, 1971; Konopka et al., 1997). In some genera, gametophyte characters can vary substantially between species (e.g., *Pogonatum* P. Beauv.; Smith, 1971; Hyvönen, 1989). Because of this, gametophyte characters have been considered, in general, less reliable taxonomically for the Polytrichaceae, at the genus level. In this context, the taxonomic placement of *Meantoinea*, a polytrichacean known only from gametophytes, has to be considered carefully. On the one hand, the differences between *Meantoinea* and other polytrichaceous genera are not greater than the intrageneric gametophyte variation seen in the most heterogeneous polytrichaceous genera. This would suggest that separation of *Meantoinea* as a distinct genus may not be warranted. On the other hand, most polytrichaceous genera do not show nearly as much variation in gametophyte morphology. Moreover, gametophyte characters are a significant component of most generic concepts in the family. In this context, separation of *Meantoinea* as a distinct genus is justified not only by the significant differences between the gametophytes of this moss and those of all known Polytrichaceae, but also by the fact that *Meantoinea* combines features of several polytrichaceous genera (Table 1).

Polytrichaceous mosses in the fossil record—The family Polytrichaceae has a surprisingly rich fossil record, with three genera described from Cenozoic and Cretaceous records (Table 2). *Eopolytrichum antiquum* is based on charcoalified sporophyte material from the Campanian (Late Cretaceous) of Georgia (Konopka et al., 1997). If the gametophyte material in the same assemblage, which exhibits polytrichaceous features, represents the same species, then *E. antiquum* is the most completely known fossil polytrichacean. *Eopolytrichum* combines features of derived peristomate Polytrichaceae (*Polytrichum* Hedwig sect. *Polytrichum* and sect. *Juniperifolia*) with features of a basal eperistomate grade (*Alophosia*, *Lyellia*, and *Bartramiopsis*) (Konopka et al., 1997; Hyvönen et al., 2004; Bell and Hyvönen, 2008, 2010). The most recent phylogenetic study of the Polytrichaceae to include *E. antiquum* (Hyvönen et al., 2004) recovered the fossil in a clade with *Polytrichum*, suggesting that *Eopolytrichum* secondarily lost its peristome and convergently evolved similarities with the basal eperistomates. However, support for the *Eopolytrichum* + *Polytrichum* clade is low (Hyvönen et al., 2004; Bell et al., 2015).

All other fossil Polytrichaceae are known only from gametophytes. Most of these fossils are preserved in Middle Eocene Baltic amber (Wolfe et al., 2016). The amber fossils include several species of the extant genus *Atrichum* P. Beauv., as well as two species of the polytrichaceous form genus *Polytrichites* (Table 2). Except for *A. mamillosum* Frahm, which exhibits mamillose cells in the lamina and lamellae, unlike any extant *Atrichum*, the fossil *Atrichum* species described from amber are very similar to extant species (Frahm, 2004). Three *Polytrichum* species listed by Göppert (1853) have no descriptions and are considered invalid (Tropicos.org, Missouri Botanical Garden, 10 July 2016, http://www.tropicos.org).

Two other species of *Polytrichites* have been described from Tertiary rocks. *Polytrichites spokanensis* Britton, a compression reported from the Miocene Latah Formation of Washington State, cannot be reliably assigned to the Polytrichaceae (or any other group of acrocarpous mosses) because of insufficient taxonomically diagnostic characters (Knowlton, 1926). *Polytrichites aichiensis* Yasui is an anatomically preserved stem fragment from the Upper Tertiary of Japan (Yasui, 1928). This fossil has a central strand with both hydroids and leptoids, a feature unique to the Polytrichaceae, but lacks any other taxonomically informative characters (Smith, 1971; Hébant, 1977).

A fossil exhibiting some similarity with the Polytrichaceae, *Livingstonites gabrielae* Vera, is known from permineralized moss gametophytes discovered in the Aptian of Antarctica (Vera, 2011). *Livingstonites* is described as an *incertae sedis* member of the basal acrocarp grade. The moss has a strong costa with complex anatomy including a band of deuters and at least one abaxial stereid band, which are found in several moss lineages, including the Polytrichaceae. Additionally, a leaf cross section (figs. 4 and 5 of Vera, 2011) of *Livingstonites* may show low lamellae typical of polytrichaceous leaves at the intersection between leaf blade and sheathing leaf base. Further detailed examination of these structures in *Livingstonites* is necessary to determine whether this moss is indeed a polytrichacean.

Meantoinea alophosioides is ca. 50 Myr older than any other unequivocal Polytrichaceae, thus providing a hard minimum age of 136 Myr for the family. This species is only the second report of pre-Cenozoic Polytrichaceae and documents the best-characterized fossil polytrichaceous gametophytes, with details of internal anatomy, leaf morphology, and asexual reproduction. The exquisite preservation of *M. alophosioides* supports the ideas that bryophytes have better preservation potential than previously thought and that the scarcity of pre-Cenozoic bryophyte fossils reflects primarily a lack of bryological expertise in the paleobotanical community rather than a paucity of fossils (Tomescu, 2016). *Meantoinea alophosioides* also expands the diversity of thoroughly characterized bryophytes in the Apple Bay flora to two families: the Tricostaceae (a family of extinct pleurocarpous mosses; Shelton et al., 2015) and the Polytrichaceae. A diverse array of permineralized fossil mosses from Apple Bay, including more species of Polytrichaceae, awaits further description (Tomescu, 2016).

Gemmae in the fossil record—Gemmae have been documented in the fossil record in both liverworts and mosses. *Naiadita lanceolata* Brodie provides the oldest unequivocal evidence of liverwort gemmae in the fossil record. *Naiadita* is a leafy liverwort abundant in the Rhaetian (Late Triassic) of England and produces terminal gemma cups on gemmiferous shoots that are ubiquitous in the fossil layers (Harris, 1939). The gemma cups are composed of numerous leaves and contain sessile gemmae ca. 400 μm in diameter. The gemmae are lenticular with an oval outline and four cells across; they have a unistratose margin and are two cells thick at the center.

Marchantites huolinhensis Li et Sun is a complex thalloid liverwort preserved as compressions with cuticular preservation from the Lower Cretaceous (Valanginian-Hauterivian) of China (Li et al., 2014). *Marchantites huolinhensis* bears gemma cups with an elliptical to circular outline, 1.1–2.5 mm in diameter. The content of the cups is incompletely preserved, and gemmae could not be identified unequivocally. The gemma cups of *M. huolinhensis* are nevertheless compelling, and this fossil represents the oldest record of such structures in a thalloid liverwort. Anatomically preserved discoid gemmae from mid-Cretaceous deposits in Australia have been described as *Marchantites marguerita* Dettman et Clifford (2000). Preserved as dispersed fossils, these uni- to bistratose gemmae are 160–440 μm across and are borne on short unicellular stalks 60 μm in diameter. Additionally, the gemmae bear a meristematic peripheral
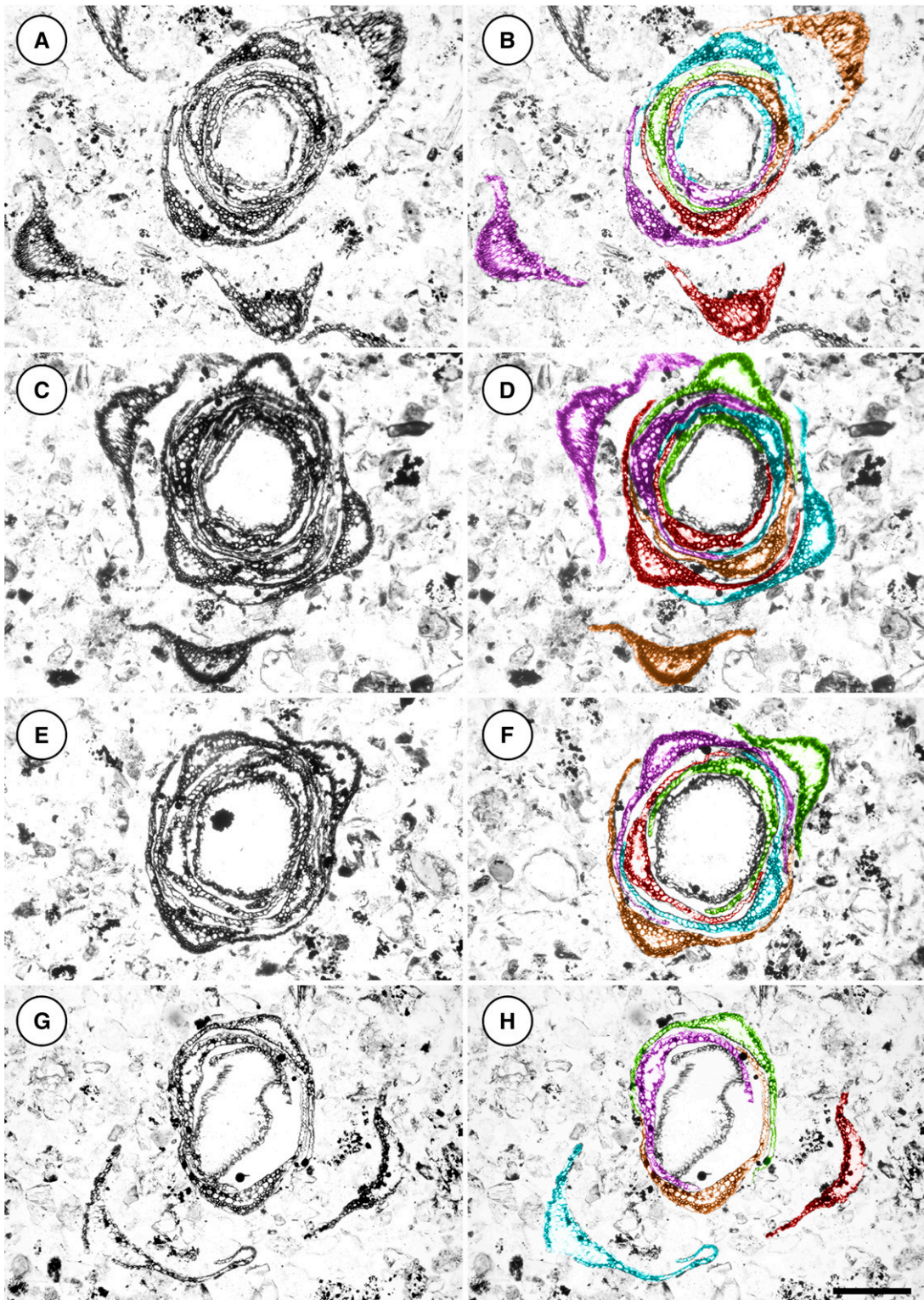
FIGURE 3 Phyllotaxis and gemma cup morphology of *Meantoinea alophosioides* gen. et. sp. nov. Apical (A, B) to basal (G, H) series of cross sections of same shoot showing leaves with 3/5 phyllotaxis and five orthostichies colored purple, orange, green, red, and blue (in B, D, F, H); note increasing leaf density from basal part (G, H) toward apical gemmae cup and reflexed leaf blades around margin of gemmae cup (compare C, D to A, B). P15393 Bbot #7b (A) Cross section of distal portion of gemmiferous shoot, showing densely packed sheathing leaf bases; scale bar for all images = 200 µm; P15393 Bbot # 7b (A, B), #20b (C, D), #27b (E, F), #41b (G, H).
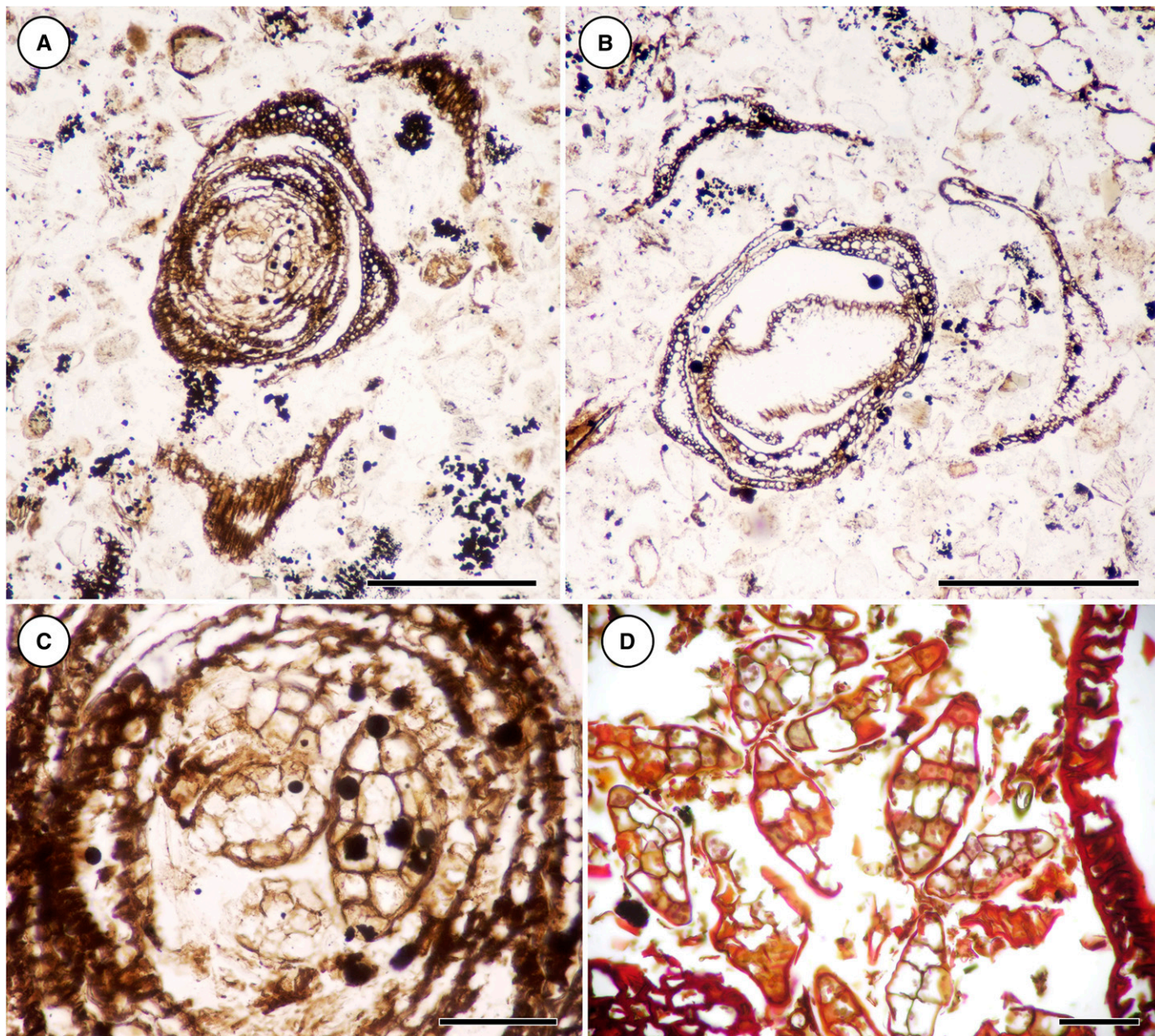
FIGURE 4 Gemmae and gemma cup of *Meantoinea alophosioides* gen. et. sp. nov. and comparison with gemmae of *Tetraphis pellucida*. (A) Cross section of *M. alophosioides* gemma cup with gemmae inside; scale bar = 250 μm; P15393 Bbot # 1b. (B) Cross section of vegetative region of same shoot, showing far fewer leaves than in specialized part of shoot that comprises gemma cup; scale bar = 250 μm; P15393 Bbot # 41b. (C) Detail of A, showing four gemmae; one gemma attached to rhizoid-like stalk; scale bar = 50 μm; P15393 Bbot # 1b. (D) Cross section of *Tetraphis pellucida* gemmae cup, showing details of gemma anatomy; scale bar = 50 μm.

notch on either side. The small size, discoid shape, unicellular stalk, and paired peripheral meristems are features shared with extant *Marchantia* L. and *Lunularia* Adanson gemmae, indicating that these fossils are the gemmae of a complex thalloid liverwort.

Another liverwort occurrence, from the Lower Cretaceous (Aptian-Albian) of Spain, has been reported to include specimens bearing gemma cups, as well as dispersed gemmae (Diéguez et al., 2007). However, in our opinion additional, better preserved specimens are required to provide unequivocal evidence for the two types of structures and, hence, for the inferred marchantiacean affinities of these fossils.

For mosses, the oldest unequivocal report of fossil gemmae is represented by two species of *Bulbosphagnum* Maslova, Ignatiev, Mosseichik et Ignatov (2016) described from the Upper Permian of Russia. *Bulbosphagnum* is a morphogenus for protosphagnalean gemmae (brood bodies) comparable to those of extant *Oedipodium* Schwägr. The gemmae are characterized by globose to oblong morphology and are produced on the costa of leaves and, possibly, on stems. They feature abundant multicellular rhizoids with oblique cross walls, and some bear developing gametophyte shoots.

The only other reports of moss gemmae come from three species of *Calymperes* Swartz (Calymperaceae) described from
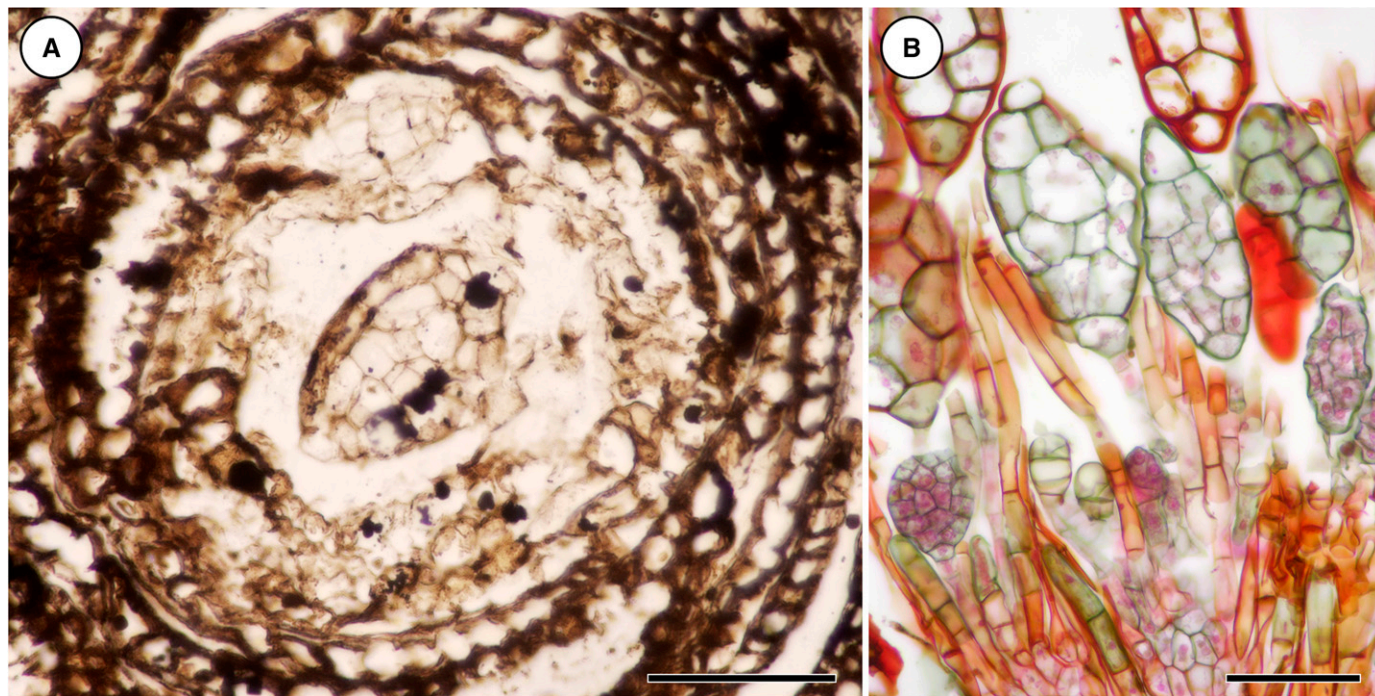
FIGURE 5 Gemmae of *Meantoinea alophosioides* gen. et. sp. nov. and comparison with gemmae of *Tetraphis pellucida*. (A) Cross section of median region of *M. alophosioides* gemma; scale bar = 50 µm; P15393 Bbot #3b. (B) Longitudinal section of *T. pellucida* gemma cup showing rhizoid-like stalks that bear gemmae and numerous immature gemmae; scale bar = 50 µm.

Early-Middle Miocene Dominican amber (Iturralde-Vinent and MacPhee, 1996). Specimens referred to the extant species *Calymperes palisotii* Schwägrichen were the first moss fossils discovered with gemmae (Frahm and Reese, 1998). This moss, like all extant species of *Calymperes*, bears a terminal cluster of fusiform to clavate gemmae adaxially on leaf apices (Reese, 2007). Gemmiferous specimens belonging to two additional extant species of *Calymperes* (*C. levyanum* Bescherelle and *C. smithii* Bescherelle) have subsequently been reported from Dominican amber (Frahm and Newton, 2005).

Cup-like structures have been reported in *Palaeocampylopus buragoae* Ignatov et Shcherbakov, a *Campylopus*-like moss from the Early Permian of Russia (Ignatov and Shcherbakov, 2009). Similarities with the perigonia of *Campylopus* Brid. have led the authors to describe these structures as putative perigonia, but they could alternatively represent terminal gemma cups. However, because *Palaeocampylopus* is preserved as compression fossils that do not show anatomical detail, the nature of the cup-like structures cannot be determined with certainty.

Meantoinea alophosioides provides the first unequivocal fossil record of gemma cups containing gemmae, in mosses. These also represent the only record of such moss structures for the Mesozoic. The gemmae of *Meantoinea* are remarkably similar in anatomy and morphology to those of the extant species *Tetraphis pellucida* (Fig. 4). This demonstrates that gemma cups formed from modified leaves, as well as gemmae very similar to those of extant species, had evolved in mosses by the Early Cretaceous. While *Naiadita* demonstrates that the leafy liverworts had evolved gemma cups by the Triassic, no extant leafy liverworts have similar gemma cups formed from modified leaves. The complex thalloid liverworts from China and Australia (*Marchantites huolinhensis* and *M. marguerita*; Li et al., 2014; Dettman and Clifford,

2000) indicate that gemma cups anatomically and morphologically similar to those of extant species had evolved in the group by the mid-Cretaceous. In light of this fossil record, it is possible that gemma cups evolved independently in both liverworts and mosses by the Mesozoic and have persisted, virtually unchanged, to the present.

***Molecular clock calibrations and the fossil record of Polytrichaceae*—** As pointed out by Wilf and Escapa (2014, 2016), in a phylogenetic context, fossils have dual utility in studies addressing the age of lineages. On the one hand, new fossil discoveries serve as independent direct tests for existing divergence age estimates. On the other hand, when incorporated as calibration points, these fossils can be used to improve the precision of such estimates.

Most fossil Polytrichaceae are known from Eocene Baltic amber and are, thus, not useful in attempts to date deep phylogenetic divergences in a group whose evolutionary history extends far beyond the Eocene, into the Mesozoic (Bell et al., 2015). The only fossils that can provide critical calibration points in the Mesozoic are *Eopolytrichum antiquum* and *Meantoinea alophosioides*. Unfortunately, the phylogenetic position of *E. antiquum* as part of a clade with *Polytrichum* is weakly supported (Hyvönen et al., 2004; Bell et al., 2015); therefore, the usefulness of *E. antiquum* as a calibration point for that clade is limited. Additionally, if *Eopolytrichum* is a close relative of *Polytrichum*, then, as a highly derived member of the Polytrichaceae, it cannot provide a reliable divergence age estimate for the family as a whole. On the other hand, *M. alophosioides* is closely similar to basal members of the Polytrichaceae (*Alophosia*, *Lyellia*, *Bartramiopsis*). This suggests that *Meantoinea* may occupy a deeper-diverging position in the family and, therefore, may provide a more useful calibration point for deep divergences within the Polytrichaceae.
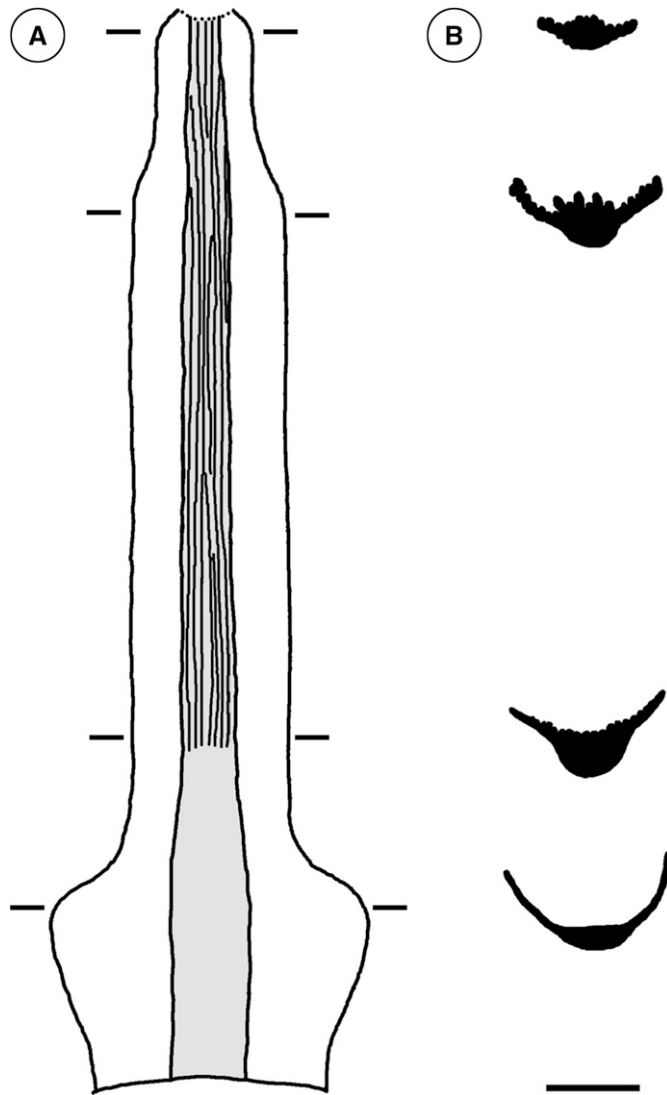
FIGURE 6 *Meantoinea alophosioides* gen. et. sp. nov. leaf model. (A) Overall leaf morphology. Note short, broad sheathing base; narrower, long leaf blade. Photosynthetic lamellae on adaxial surface of costa (gray), along leaf blade. Leaf apex incompletely preserved. (B) Series of leaf cross sections at four levels along leaf; from base to tip, sections correspond to specimens illustrated in Fig 1A, 2H, 1F, and 2G. Scale bar = 250 μm.

If *Eopolytrichum*, a Campanian (ca. 83 Ma) moss, is a derived member of the Polytrichaceae, and *Meantoinea*, a Valanginian (ca. 136 Ma) moss, occupies a position close to the base of the Polytrichaceae, then it is possible that significant evolutionary radiation leading to the emergence of many extant genera occurred during the Cretaceous. Irrespective of this, as the oldest unequivocal Polytrichaceae, *Meantoinea* provides a minimum hard age for the group, which certainly arose prior to the Valanginian, 140 Myr. A recent study addressing the tempo of evolution across all of bryophyte phylogeny has proposed that the Polytrichopsida (i.e., the class whose sole family is Polytrichaceae) emerged between 297 and 471 Ma (Laenen et al., 2014, supplementary information, p. 118). Whereas the older end of this interval reflects a choice to constrain the age of crown embryophytes at 815 Ma, the younger end of the interval is based on the age of the Early Permian moss *Palaeocampylopus buragoae* (273 Ma; Ignatov and Shcherbakov, 2009), as a stem polytrichopsid. This choice is intriguing, given that *P. buragoae* lacks features that allow unambiguous assignment to the Polytrichopsida and is, in fact, considered to show closer affinities with the Dicranaceae (Ignatov and Shcherbakov, 2009), a family within class Bryopsida. The 297 Myr age of stem Polytrichopsida, obtained by calibration using *P. buragoae*, raises questions, as it is more than twice as old as any known unequivocal polytrichopsid. *Meantoinea* adds a new calibration point for the deeper-diverging Polytrichaceae, providing another constraint for estimating clade age in future studies of the tempo of bryophyte evolution.

CONCLUSIONS

Anatomically preserved mosses are exceptionally rare in pre-Cenozoic rocks (Smoot and Taylor, 1986; Konopka et al., 1997, 1998; Hübers and Kerp, 2012; Hedenäs et al., 2014; Tomescu, 2016). Given this meager record, fossils are generally not considered to be very valuable for understanding moss evolution. In this context, *Meantoinea alophosioides* provides an important addition to a growing body of evidence suggesting that fossils are crucial for understanding moss phylogeny. We emphasize that a diverse anatomically preserved fossil bryoflora is preserved in the Early Cretaceous Apple Bay locality of Vancouver Island, Canada (Tomescu, 2016). *Meantoinea* is the third moss described in detail from this locality, broadening the taxonomic diversity of the Apple Bay bryoflora to include the Polytrichaceae in addition to the extinct hypnanaean family Tricostaceae (Shelton et al., 2015, 2016). *Meantoinea* also marks the oldest unequivocal record of Polytrichaceae, providing a hard minimum age of ca. 136 Myr (Valanginian) for the family and the first record of fossil moss gemma cups.

Meantoinea preserves a high level of anatomical and morphological detail, based on multiple anatomically preserved gametophyte shoots. This level of detailed information is known from only a handful of other pre-Cenozoic moss fossils (Smoot and Taylor, 1986; Ko-

TABLE 1. *Meantoinea* compared with polytrichaceous mosses with similar features.

	Meantoinea	*Alophosia*	*Bartramiopsis*	*Lyellia*	Gametophytes associated with *Eopolytrichum*
Adaxial photosynthetic lamellae	Present	Absent	Present	Present	Present
Lamellae distribution	Costa	—	Costa	Costa	Costa + lamina
Lamellae height	2–3 cells	—	4–8 cells	6–8 cells	3–4 cells
Lamella marginal cell	Mamillose	—	Undifferentiated	Mamillose	Undifferentiated to mamillose
Gemmae	Present	Present	Absent	Absent	Absent
Bistratose lamina	Present	Present	Present	Present	Absent
Mamillose laminar cells	Present	Present	Present	Present	Absent
Leaf margin	Single unicellular teeth	Single multicellular teeth	Single multicellular teeth	Double multicellular teeth	Single unicellular teeth

TABLE 2. Polytrichaceous moss fossils.

Species	Age	Stratigraphy	Location	Preservation	Assignment to Polytrichaceae	References
Polytrichites aichiensis	Upper Cenozoic	?	Aichi, Japan	Permineralized	Unequivocal	Yasui, 1928
Polytrichites spokanensis	Miocene	Latah Formation	Washington, USA	Compression	Equivocal; branched shoot, no obvious photosynthetic lamellae	Knowlton, 1926
Atrichum subrhystophyllum	Eocene	Baltic amber	—	Amber	Unequivocal	Frahm, 2004, 2010
Atrichum groehnii	Eocene	Baltic amber	—	Amber	Unequivocal	Frahm, 2004, 2010
Atrichum mamillosum	Eocene	Baltic amber	—	Amber	Unequivocal	Frahm, 2004, 2010
Polytrichites pogonatoides	Eocene	Baltic amber	—	Amber	Unequivocal	Frahm, 1999, 2010
Polytrichites convolutus	Eocene	Baltic amber	—	Amber	Equivocal; photosynthetic lamellae not visible	Mägdefrau, 1957; Frahm, 2010
Eopolytrichum antiquum and associated gametophytes	Late Cretaceous (Campanian)	Gaillard Formation	Georgia, USA	Charcoalified	Unequivocal	Konopka et al., 1997
Meantoina alophosioides	Early Cretaceous (Valanginian)	Longarm Formation equivalent	Vancouver Island, Canada	Permineralized	Unequivocal	this study

nopka et al., 1997, 1998; Shelton et al., 2015, 2016). Detailed anatomical and morphological information on fossil mosses serves two important purposes. First, it allows accurate taxonomic placement, which is not always obtainable for fossils (Crepet et al., 2004), thus contributing significantly to understanding of pre-Cenozoic moss diversity. Second, it is a prerequisite for any attempt to address the deep phylogeny of mosses circumventing the taxon sampling issues that plague "extant-only" phylogenies (e.g., Rothwell and Nixon, 2006; Rothwell et al., 2009). Study of fossil species that preserve high levels of morphological and anatomical detail broadens the range of taxon sampling by adding novel combinations of characters whose existence could not have been foreseen from studies based exclusively on extant plants. Every time phylogenetic studies have sampled systematically the fossil record, their results have provided new perspectives (e.g., Rothwell, 1999; Rothwell and Nixon, 2006; Hilton and Bateman, 2006). This second purpose is particularly relevant, since fossil information is crucial for understanding the evolution of a group such as the Polytrichaceae, which lack close living relatives. When incorporated in phylogenetic studies, *Meantoinea* may provide some of the information needed to confidently resolve the phylogenetic position of Polytrichaceae with respect to other moss lineages.

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