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Grimmiaceae in the Early Cretaceous: *Tricarinella crassiphylla* gen. et sp. nov. and the value of anatomically preserved bryophytes

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- **Background and Aims** Widespread and diverse in modern ecosystems, mosses are rare in the fossil record, especially in pre-Cenozoic rocks. Furthermore, most pre-Cenozoic mosses are known from compression fossils, which lack detailed anatomical information. When preserved, anatomy significantly improves resolution in the systematic placement of fossils. Lower Cretaceous (Valanginian) deposits on Vancouver Island (British Columbia, Canada) contain a diverse anatomically preserved flora including numerous bryophytes, many of which have yet to be characterized. Among them is the grimmiaceous moss described here.
- **Methods** One fossil moss gametophyte preserved in a carbonate concretion was studied in serial sections prepared using the cellulose acetate peel technique.
- **Key Results** *Tricarinella crassiphylla* gen. et sp. nov. is a moss with tristichous phyllotaxis and strongly keeled leaves. The combination of an acrocarpous condition (inferred based on a series of morphological features), a central conducting strand, a homogeneous leaf costa and a lamina with bistratose portions and sinuous cells, and multicellular gemmae, supports placement of *Tricarinella* in family Grimmiaceae. *Tricarinella* is similar to *Grimmia*, a genus that exhibits broad morphological variability. However, tristichous phyllotaxis and especially the lamina, bistratose at the base but not in distal portions of the leaf, set *Tricarinella* apart as a distinct genus.
- **Conclusions** *Tricarinella crassiphylla* marks the oldest record for both family Grimmiaceae and sub-class Dicranidae, providing a hard minimum age (136 million years) for these groups. The fact that this fossil could be placed in an extant family, despite a diminutive size, emphasizes the considerable resolving power of anatomically preserved bryophyte fossils, even when recovered from allochthonous assemblages of marine sediments, such as the Apple Bay flora. Discovery of *Tricarinella* re-emphasizes the importance of paleobotanical studies as the only approach allowing access to a significant segment of biodiversity, the extinct biodiversity, which is unattainable by other means of investigation.

Key words: Cretaceous, fossil, moss, acrocarpous, Grimmiaceae, Dicranidae, anatomical preservation, *Tricarinella crassiphylla*.

INTRODUCTION

Both the phylogenetic position of mosses on the embryophyte tree (Mishler and Churchill, 1985; Laenen *et al.*, 2014) and their considerable diversity in modern ecosystems [approx. 13 000 species, according to Goffinet *et al.* (2009), or 7000–8000, as reported by Hyvönen *et al.* (2004)] predict a rich and ancient fossil record for the clade. These data also suggest that a great deal of evolution occurred during the Paleozoic and Mesozoic (Hübers and Kerp, 2012; Oostendorp, 1987; Tomescu, 2016). Therefore, it is surprising that mosses are exceptionally rare in pre-Cenozoic rocks (Taylor *et al.*, 2009), with the fossil record presently offering little insight into the deeper history of moss evolution. In this context, it is encouraging that an Early Cretaceous fossil flora at Apple Bay, on Vancouver Island (British Columbia, Canada), hosts several new mosses and

other bryophytes, including the oldest unequivocal pleurocarps (Shelton *et al.*, 2015, 2016), polytrichaceous mosses (Tomescu, 2016; Bippus *et al.*, 2017), and others that await detailed description. With its unparalleled diversity of anatomically preserved bryophytes (Tomescu, 2016), the Apple Bay flora is providing a broad perspective onto pre-Cenozoic moss diversity and an excellent opportunity to address Mesozoic moss evolution.

Acrocarpous mosses, which occupy basal positions in the clade (Laenen *et al.*, 2014), would have diversified significantly by the Early Cretaceous. Thus, detailed characterization of the Apple Bay flora promises to reveal considerable additional extinct diversity of acrocarpous mosses. In modern floras, the Grimmiaceae are a relatively speciose lineage of acrocarpous mosses (at least 325 species; Ignatova and Muñoz, 2004; Hastings and Ochyra, 2007) with a worldwide geographic

distribution. Grimmiaceous mosses usually form tufts or cushions on exposed rock surfaces and are readily recognizable by their thick-walled, sinuous to nodulose mid-leaf cells (Hastings and Ochyra, 2007). The phylogenetic position of Grimmiaceae within sub-class Dicranidae is well resolved (Chang and Graham, 2014). The family traditionally includes the cosmopolitan and heterogeneous genera *Grimmia* Hedw. and *Racomitrium* Brid. (Hastings and Ochyra, 2007). Taxonomic circumscription of the family, and especially of these two genera, has fluctuated widely (Ignatova and Muñoz, 2004; Hastings and Ochyra, 2007; Hernández-Maqueda *et al.*, 2008). Despite the abundance and widespread modern distribution of Grimmiaceae, the family is represented by a single fossil occurrence reported from Eocene Baltic amber (Frahm and Gröhn, 2013). This leaves our understanding of early grimmiaceous evolution and diversity without a grounding in the fossil record.

Here we describe an anatomically preserved moss assigned to family Grimmiaceae, based on a permineralized gametophyte shoot from the Lower Cretaceous at Apple Bay. This fossil, described as a new genus and species, combines tristichous phyllotaxis, keeled leaves with a homogeneous costa, basally bistratose and distally unistratose lamina, sinuous lamina cells and irregularly shaped gemmae. This moss is the only pre-Cenozoic fossil representative of family Grimmiaceae and the oldest moss unequivocally assignable to sub-class Dicranidae, providing a hard minimum age of 136 million years (Ma) for the family and subclass. Remarkably, despite being represented only by one incompletely preserved gametophyte segment <0.5 cm long, this fossil yields sufficient characters for assignment to the Grimmiaceae. This discovery thus highlights the resolving power of anatomical preservation in the taxonomic placement of fossils, particularly mosses.

MATERIALS AND METHODS

The moss material is preserved by cellular permineralization in a calcium carbonate concretion, as part of an allochthonous fossil assemblage deposited in nearshore marine sediments. Concretions are included in greywacke beds exposed on the northern shore of Apple Bay, Quatsino Sound, located on the west side of Vancouver Island, British Columbia, Canada (50°36′2″N, 127°39′25″W; UTM 9U WG 951068) (Stockey and Rothwell, 2009). Layers containing the concretions were regarded as Longarm Formation equivalents (Jeletzky, 1976) but have been dated by oxygen isotope analyses to the Valanginian (Early Cretaceous, approx. 136 Ma; Stockey *et al.*, 2006; D. Gröcke, personal communication, 2013). The Early Cretaceous Apple Bay flora includes lycophytes (Stockey and Rothwell, 2004), equisetophytes (Stanich *et al.*, 2009), at least ten fern families (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), numerous representatives of various seed plant groups (Stockey and Wiebe, 2008; Rothwell *et al.*, 2009; Stockey and Rothwell, 2009; Rothwell and Stockey, 2010, 2013; Klymiuk and Stockey, 2012; Atkinson *et al.*, 2014a, b; Ray *et al.*, 2014; Klymiuk *et al.*, 2015), fungi (Smith *et al.*, 2004; Bronson *et al.*, 2013) and a lichen with heteromerous organization (Matsunaga *et al.*, 2013). Moreover, this flora is probably the most diverse assemblage of fossil bryophytes known worldwide, with leafy

and thalloid liverworts and numerous moss morphotypes currently recognized (Shelton *et al.*, 2015, 2016; Tomescu, 2016; Bippus *et al.*, 2017). Pleurocarpous, polytrichaceous and leucobryaceous mosses are present, as well as several morphotypes of unknown affinities.

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, Freiburg, Germany). Micrographs were taken using a Nikon Coolpix E8800 digital camera on a Nikon Eclipse E400 compound microscope and an Olympus DP73 digital camera mounted on an Olympus SZX16 microscope. Images were processed using Photoshop (Adobe, San Jose, CA, USA). The 3-D reconstruction of the moss was generated by using Amira 6.3 software (FEI, Hillsboro, OR, USA) with tracings of serial sections photographs produced using Photoshop. All specimens and preparations are housed in the University of Alberta Paleobotanical Collections (UAPC-ALTA), Edmonton, Alberta, Canada.

We use 'cortex' and 'cortical cells' to refer to the entirety of tissue that comprises gametophyte stems, beneath the epidermis and to the exclusion of a central conducting strand.

RESULTS

Systematics

Class: Bryopsida Rothm.
Sub-class: Dicranidae Doweld
Order: Grimmiales M. Fleisch.
Family: Grimmiaceae Arn.
Genus: *Tricarinella* Savoretti, Bippus, Stockey, Rothwell et Tomescu gen. nov.
Generic diagnosis: Gametophyte three-dimensionally branched. Stem terete basally, triquetrous distally; central strand present. Phyllotaxis tristichous, helical. Leaves lanceolate, keeled. Costa homogeneous. Lamina entirely bistratose at leaf base, bistratose sectors adjacent to costa distally, marginal sectors unistratose. Bistratose sectors taper apically; lamina unistratose in apical half of leaf. Lamina cells sinuous near leaf base.
Etymology: *Tricarinella* for the strongly three-edged profile of the shoot, which is due to strongly keeled three-ranked leaves (*tri* = three; *carina* = keel; the suffix *-ella* signifies a diminutive, for the small size of the gametophyte).
Type species: *Tricarinella crassiphylla* Savoretti, Bippus, Stockey, Rothwell et Tomescu sp. nov.
Specific diagnosis: Gametophyte cushion-forming. Main shoot small, 500 μm in diameter, triangular in cross-section. Branches diverge at acute angles. Stem with sparse, small leaves basally, densely covered in leaves distally. Stem epidermis of small, flat cells. Cortex of larger, isodiametric parenchyma cells. Leaves densely imbricate along distal shoot segments; erect spreading, with basal part tightly appressed to stem. Leaves at least 600 μm wide, with keel starting close to base, more pronounced distally. Costa single, strong, crescent-shaped in cross-section basally, triangular to circular distally. Costa cells parenchymatous, circular in cross-section. Costa with abaxial layer of smaller cells throughout its length, adaxial layer of smaller cells in the distal costa. Lamina bistratose up to 130–160 μm

from leaf base, with recurved margins when unistratose; recurvation more pronounced distally. Gemmae multicellular, subspherical to irregular in shape, between stem and leaf bases.

Holotype hic designatus: Gametophyte shoot in rock slab UAPC-ALTA P13311 I (slides I top series d).

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

Stratigraphic position and age: Longarm Formation equivalent, Valanginian (approx. 136 Ma), Early Cretaceous.

Etymology: The specific epithet *crassiphylla* refers to the basally bistratose (i.e. thick) leaf lamina (*crassi* for thick; *phylla* for leaf).

Description

Branching, shoot architecture and stem anatomy. The specimen is approx. 3 mm long and represents a segment of gametophyte shoot bearing two branches (Figs 1A and 2A). The main shoot is small, barely 500 μm in diameter (including leaf bases). The stem is densely covered in leaves only along its upper half (Fig. 2B); the lower half has sparse, smaller leaves (Fig. 2E). The lower section of the stem is also thinner, approx. 200 μm in diameter. Stem diameter increases to about 240 μm at the base of the upper portion that bears dense leaves, where it is still circular in cross-section (Fig. 2C), to 276 μm at the distal end, where it is triquetrous (Fig. 2B). Two branches arise at different levels about two-thirds of the length from the base of the specimen. Branches diverge at acute angles, in two directions that form a 60 ° angle. The directions of divergence of the two branches correspond to two of the angles of the triquetrous subtending stem (Fig. 2A). Thus, branching architecture is 3-D, i.e. not complanate. These two branches are also thinner at the base (approx. 130 μm) and become thicker distally (approx. 150 μm). They maintain a circular cross-section but are only preserved for up to 1 mm.

The main stem exhibits differential preservation between its basal and distal regions. This probably reflects differences in the anatomy and, possibly, cell wall chemistry of the stem tissues, due to the specific growth habit of this moss (see Discussion below). The basal half of the stem is 200 μm in diameter and only the epidermis and central strand are preserved (Fig. 2E). Epidermal cells are globose, 6–11 μm in diameter. The central strand, approx. 40 μm across, consists of 8–11 cells of small diameter. On the upper half of the stem, epidermal cells are small (10 μm), with somewhat thicker cell walls than the cortical cells beneath (Fig. 2B). The cortex consists of larger (15 μm) isodiametric parenchyma cells with thin cell walls, forming 3–4 layers (Fig. 2D). Toward the centre of the stem there is a sharp transition from the cortex, which in this area shows darker cell walls, to a zone that lacks cellular preservation (Fig. 2D).

The two branches generally preserve only the epidermis, which is similar to the stem epidermis, and one or two layers of thinner walled cells beneath the epidermis (Fig. 2F, G). The central tissues of the branches are only preserved at the base,
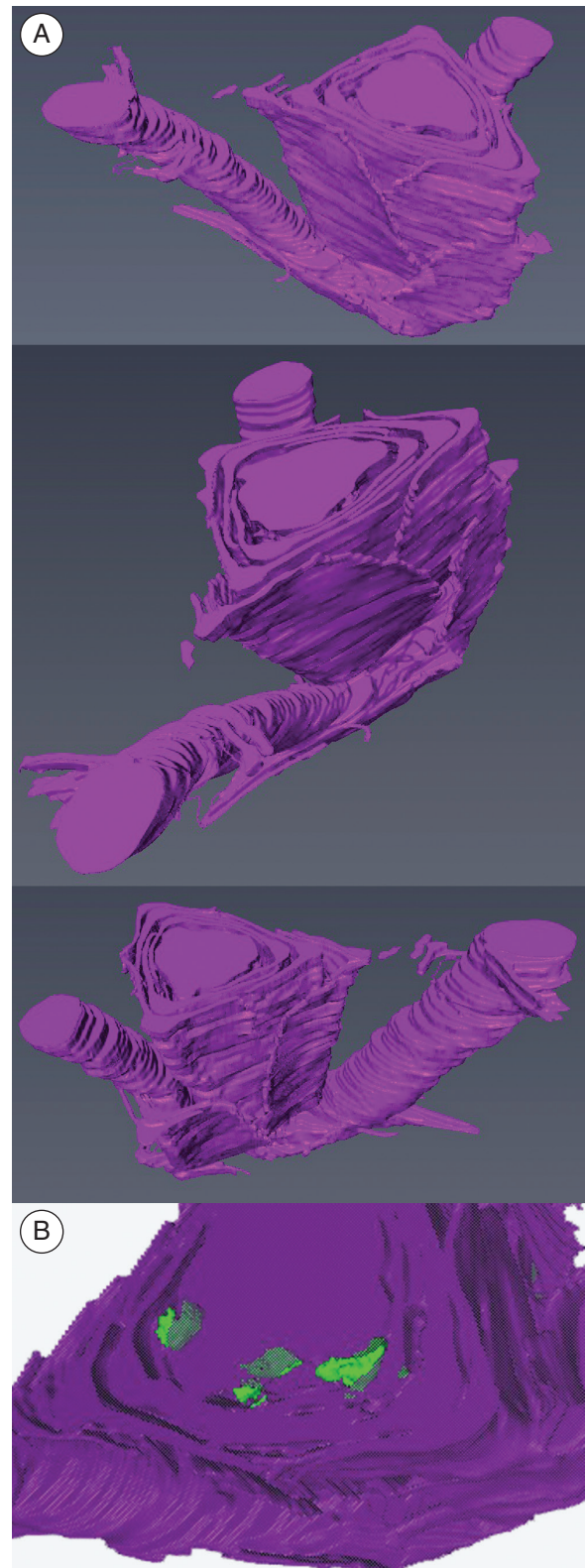

FIG. 1. Three-dimensional rendering of the upper, densely leafy stem portion of *Tricarinella crassiphylla* gen. et sp. nov. (A) Three angles of view of rendering. (B) Rendering of structures interpreted as leaf-borne gemmae.
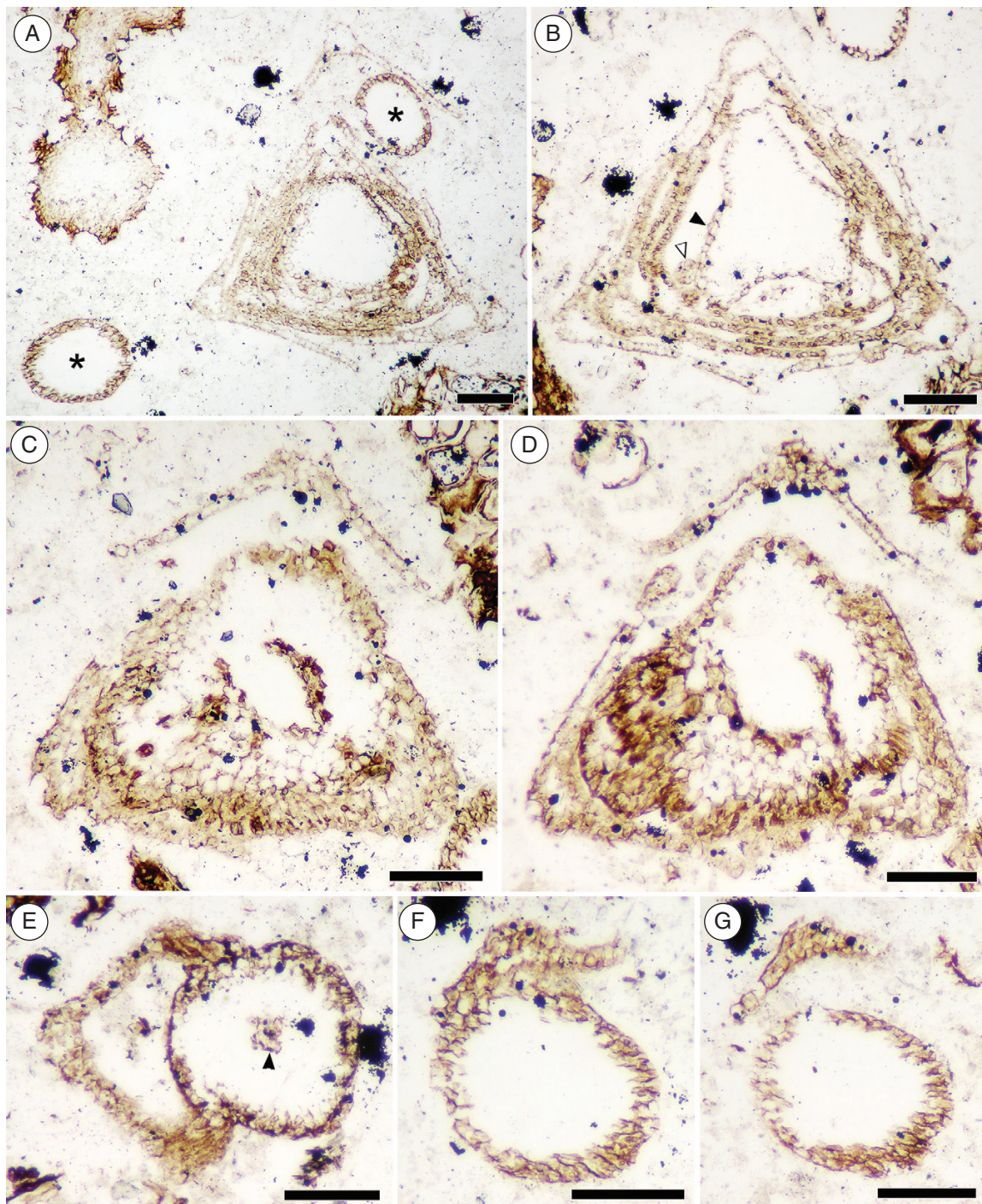
FIG. 2. Stem and branch anatomy of *Tricarinella crassiphylla* gen. et sp. nov. (A) Gametophyte shoot with the main stem and two branches (asterisks) cross-sectioned. Scale bar = 100 μm. P13311 Itop 17d. (B) Cross-section in the distal portion of the main stem; only the epidermis (black arrowhead) is preserved. Leaves in three ranks. Note the gemmae next to the lower left angle of the stem (white arrowhead) and between the lower side of the stem and the innermost leaf. Scale bar = 100 μm. P13311 Itop 9d. (C) and (D) Cross-sections of the main stem at two levels, in the transition zone between the basal leafless portion and in the densely leafed upper portion. Note the low number of leaves (compared with A and B), the base of the branch diverging on the lower left side, the large parenchymatous cortex and the open space at the centre where the central strand is not preserved. Scale bars = 100 μm. P13311 Itop 36d (C) and 33d (D). (E) Cross-section in a basal portion of the main stem, with the central strand (arrowhead) and a diverging leaf on the left; all the leaf except the margin diverged from the stem at this level. Scale bar = 100 μm. P13311 Itop 56d. (F) and (G) Cross-sections at two levels through the branch with a diverging leaf. Note the leaf costa and unistratose lamina. Scale bar = 100 μm. P13311 Itop 11d (F) and 10d (G).

where the branch connects to the stem. Here, the branches exhibit a parenchymatous cortex and a thin, inconspicuous central strand (Fig. 3A).

Leaves are erect spreading. Their basal portions are tightly appressed to the stem and distally the lamina diverges at a wider angle (Fig. 2A, B). Leaves are densely imbricate on the
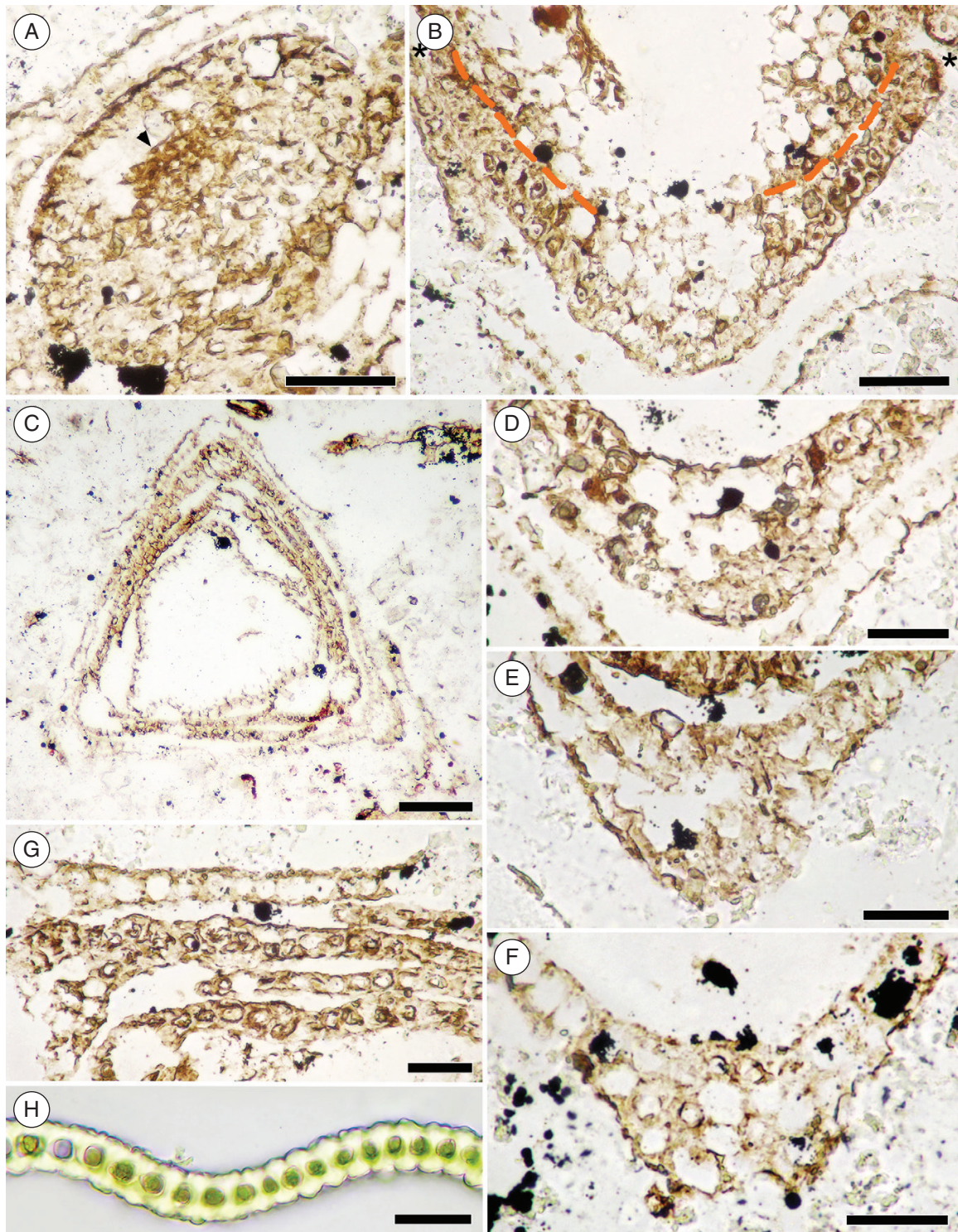
FIG. 3. Branch and leaf anatomy of *Tricarinella crassiphylla* gen. et sp. nov. (A) Cross-section of a branch base diverging from the stem (at bottom right, with larger cells). Note the conducting strand of the branch (arrowhead) with small, darker cells. Scale bar = 50 µm. P13311 Itop 32d. (B) Base of a leaf diverging from the stem. Note the larger cells of the leaf costa, the abaxial (lower) epidermis on the costa and darker cells of the leaf lamina; leaf margins are indicated by asterisks and the dashed line marks the boundary between the stem and leaf. Scale bar = 50 µm. P13311 Itop 30d. (C) Cross-section of a distal portion of the stem emphasizing sharply keeled leaves with a tristichous arrangement, lending a triangular outline to the shoot. Note the triquetrous stem. Scale bar = 100 µm. P13311 Itop 3d. (D–F) Basal (D) to apical (F) series of cross-sections through leaf costa. Note the large cells of the costa, the abaxial (lower) epidermis (D, E), the adaxial (upper) epidermis (E, F), the bistratose lamina (D), gradual transition to a unistratose lamina (E) and sharp transition to a unistratose lamina (F). Scale bars = 30 µm. P13311 Itop 26d (D), 30d (E), 31d (F). (G) Cross-sections of several adjacent leaf laminae emphasizing the contrast between sinuous cells in the lower leaf lamina (lower three leaves) and the non-sinuous cells of the upper lamina (top leaf). Scale bar = 30 µm. P13311 Itop 16d. (H) Cross-section of the leaf lamina of *Racomitrium varium* with sinuous cells (courtesy of David H. Wagner; www.fernzenmosses.com); compare with the sinuous and non-sinuous lamina cells of *Tricarinella* in (G). Scale bar = 30 µm.

main stem. Ten leaves arise from the stem over 3 mm of length. Leaves are helically arranged and form three ranks: tristichous phyllotaxis (Fig. 2A, B). Only one leaf base (Fig. 2F, G) is preserved on the two branches; it is approx. 500 µm wide and its anatomy is similar to that of the main stem leaves. In this respect, the branches are similar to the basal part of the main stem, characterized by a circular cross-section and distantly spaced small leaves (Fig. 2E).

Leaf morphology and anatomy. Leaves have an overall lanceolate shape. They are 400 µm wide at the point where their base is distinguishable from the stem, but still attached to the latter (Fig. 3B). Leaves are widest (up to 625 µm) near the base and taper gradually toward the tip. Leaf tips are missing due to incomplete preservation that probably reflects abrasion during transport, prior to deposition; the short basal lengths of branches preserved are also consistent with abrasion during transport. Leaves are keeled starting close to the base, with the keel formed along the strong single costa (Fig. 4A). As a result, they are V-shaped in cross-section, becoming narrower apically, with angles as low as 68 ° between the two sides of the lamina. The sharply keeled leaves and their tristichous arrangement lend the shoot a triangular cross-section with three pronounced edges (Fig. 3C).

The costa is homogeneous and has a profile that varies along the leaf, from slightly adaxially concave and 66 µm thick, at the base, to triangular at mid-leaf, and circular (60 µm thick), bulging abaxially, closer to the tip (Fig. 4A). In leaf cross-sections, cells of the costa are isodiametric, thin walled, up to 18 µm in diameter (Fig. 3D). The cells exhibit only small variation in size and show no pattern of organization other than a weakly differentiated epidermis. Cells of the abaxial costa epidermis tend to be smaller (14 µm), with somewhat thicker walls (Fig. 3E). The same type of smaller, thicker walled cells form an adaxial costa epidermis in distal parts of the leaf (Fig. 3F). Laterally, the transition between costa and lamina is abrupt in distal portions of the leaves and becomes progressively less distinct basally (Figs 3F and 4A). This is due to variations in lamina thickness: bistratose in basal portions of the leaves and unistratose in the distal portions.

The lamina is entirely bistratose at the leaf base and up to 28.8 µm thick (Fig. 4A). Distally, beyond 120–160 µm from the leaf base, the lamina consists of bistratose sectors adjacent to the costa, and unistratose marginal sectors. The width of the bistratose sectors tapers apically and the lamina is entirely unistratose (13.2 µm thick) in the apical half of the leaf, at approx. 750 µm from the base. The unistratose lamina exhibits recurved margins with an increasingly more pronounced curvature apically (Fig. 4A). Cells in the basal part of the lamina have sinuous walls, as indicated by the variable size and irregular distribution (over small scales) of cell lumens (Fig. 3G), that replicate observations on extant mosses (Fig. 3H). Contrasting this anatomy, cells in the upper portions of the unistratose lamina have significantly thinner, non-sinuous walls (Fig. 3G).

Small structures that appear multicellular occur between the stem and leaves, in the upper part of the gametophyte shoot (Figs 1B and 2B). They have sub-spherical to irregular shapes, up to 225 µm long. One of them exhibits a regular, circular cross-sectional outline consisting of approx. 20 cells, each about 60–70 µm in diameter (Fig. 4B); another one has an oval cross-sectional outline, thin-walled cells around the periphery and darker cells at the centre (Fig. 4C).
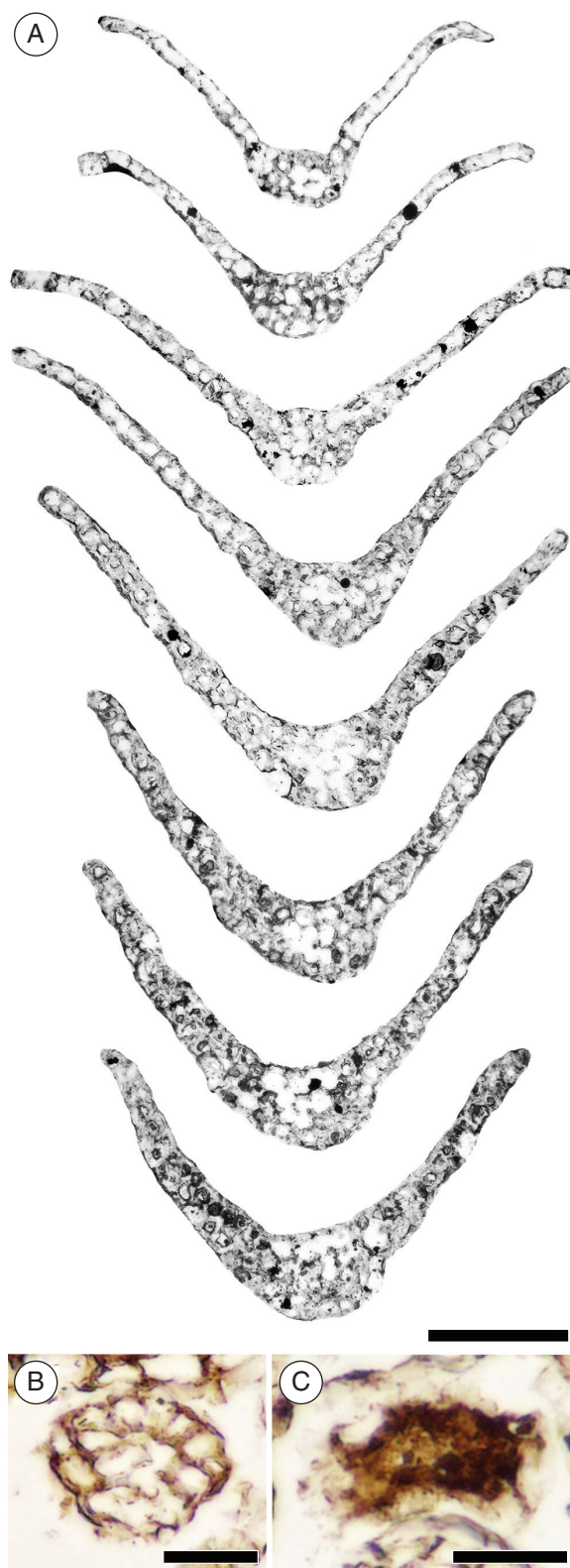

FIG. 4. (A) Series of selected sections illustrating changes in anatomy and morphology of *Tricarinella crassiphylla* leaves from the base (bottom) to the tip (top). Scale bar = 100 µm. From base to tip: P13311 Itop 28d, 26d, 25d, 29d, 24d, 36d, 32d and 25d. (B) and (C) Details of gemmae located between the main stem and leaves. (B) Section of a round gemma with cellular detail. Scale bar = 20 µm. P13311 Itop 8d. (C) Section of a gemma with a dark centre. Scale bar = 20 µm. P13311 Itop 8d.

DISCUSSION

Anatomy, morphology and growth habit

The central tissues of *Tricarinella* are preserved to a variable degree along the main stem. In some parts of the specimen (especially the upper parts), all stem tissues except the epidermis are missing (Fig. 2B); other parts exhibit cellular preservation close to the centre of the stem. In these cases, a sharp transition is conspicuous between inner layers of the cortex, consisting of smaller cells with darker (thicker) walls, and a central zone that lacks cellular preservation entirely (Fig. 2D). This suggests that the cells in this central zone had comparatively lower preservation potential and thus were delicate with thinner walls. These features are similar to those of cells that comprise conducting strands of living mosses (e.g. Murray, 1984, figs 7, 20 and 32; Streiff, 2005, fig. 4.8; Feng *et al.*, 2013, fig. 1B). Together, these observations suggest that a central conducting strand consisting of delicate cells with low preservation potential was present in the stem of *Tricarinella*.

The leaves of *Tricarinella* have a centrally located longitudinal ridge. Laterally from this ridge, the leaves are bistratose at the base and unistratose in their upper half, with a transition zone consisting of bistratose sectors adjacent to the central ridge, which are progressively narrower distally. In some mosses (e.g. Leucobryaceae; Yamaguchi, 1993), a broad bi- to multistratose leaf costa can occupy most of the leaf width, while the unistratose lamina is very narrow (a few cells wide). In contrast to these, in *Tricarinella*, the costa is represented only by the central ridge and the bistratose portions are part of the leaf lamina. Several lines of evidence support this interpretation. First, the central longitudinal ridge is distinct, narrow but relatively strong, abaxially protruding, like a costa. Secondly, the ridge and bistratose leaf portions are anatomically distinct: whereas cells of the longitudinal ridge are large, with thin walls (as seen in leaf cross-sections), those of the bistratose leaf portions are smaller and sinuous. Thirdly, a leaf structure including a costa that is distinct from bistratose parts of the lamina (or from an entirely bistratose lamina) is present in many species scattered among various families (e.g. Amblystegiaceae, Dicranaceae, Diphysciaceae, Fissidentaceae, Grimmiaceae, Meesiaceae, Orthotrichaceae, Polytrichaceae, Pottiaceae, Ptychomitriaceae and Vittiaceae; see also below).

The small structures observed between the stem and leaves are interpreted as gemmae. They are located, in all four cases, close to leaf bases, between the stem and the adaxial side of the innermost leaf. Because of this, they are interpreted as most probably associated with leaf axils, although direct evidence for their attachment is missing. This positioning, along with their sub-spherical to irregular shapes (Fig. 1B), are most consistent with stalked axillary gemmae, like those that occur on *Grimmia torquata* Drumm. (Ignatova and Muñoz, 2004).

Tricarinella combines several features associated with an upright growth habit within tightly packed cushion-forming ramets. These include 3-D branching (e.g. the two successive branches diverging in directions that form a 120 ° angle); a steep gradient of stem morphology that transitions from a basal rhizomatous portion of significant length, bearing few or reduced leaves, to distal portions densely covered in leaves; erect-spreading leaves with bases tightly packed around the stem and imbricate; and branches characterized by long leafless basal portions although they arise from leafy sections of the main stem. While none of these features, considered separately, provides unequivocal support for a cushion-forming growth habit, together they constitute a significant weight of evidence for that interpretation. The tight packing of neighbouring upright shoots within cushions forces leaves into an erect or erect-spreading orientation. Tight cushions also limit light penetration. As a result, branches arising below the surface of the cushion do not develop strong or dense leaves along their shaded basal portions (Fig. 2E); they only start producing fully developed leaves as their growing tips approach, or reach, the surface of the cushion, thus reiterating the stem morphology gradient as the cushion expands vertically (Figs 2F, G and 5).

Taxonomic affinities of Tricarinella

Moss taxonomy at and above the family level relies to a significant extent on sporophyte characters. However, differences in gametophyte morphology have also been used successfully in taxonomic treatments, including those of fossils (Hedenäs *et al.*, 2014; Bippus *et al.*, 2017). Three prominent gametophytic features of *Tricarinella* call for appraisal in a taxonomic context: the tristichous phyllotaxis, bistratose leaf lamina and the homogeneous costa. The tristichous condition can be found in various groups of mosses (Herzog, 1916; Welch, 1960; Zander, 1993; Gradstein *et al.*, 2001; Ochyra *et al.*, 2008; Frey and Stech, 2009; Goffinet *et al.*, 2009). Species or entire genera in the following families exhibit tristichous phyllotaxis: Meesiaceae, Seligeriaceae, Bartramiaceae, Catoscopiaceae, Pottiaceae, Amphidiaceae, Ditrichaceae, Fontinalaceae,
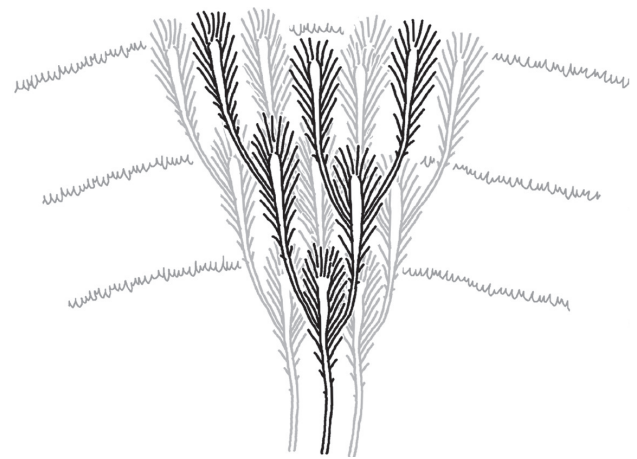

Fig. 5. The cushion-forming growth habit inferred based on a suite of morphological features of *Tricarinella crassiphylla* (3-D branching; steep gradient of stem morphology transitioning from the thinner, long basal portion bearing few reduced leaves, to distal portions densely covered in leaves; erect-spreading leaves with imbricate bases tightly packed around the stem; and branches with long leafless bases although they arise from leafy sections of the main stem). Thr eeconstruction shows two previous levels of cushion surface. The cushion expands vertically by production of branches arising from the upper leafy portions of stems and reiterate the growth habit of the main stem – a longer leafless (or with sparse small leaves) basal portion, corresponding to the low-light environment below the cushion surface, topped by a shorter densely leafy portion exposed to light at and close to the cushion surface.

Sematophyllaceae, Hypnodendraceae and Hypopterygiaceae. This broad taxonomic occurrence indicates that tristichous phyllotaxis is homoplastic.

A bistratose leaf lamina can take a number of shapes among mosses. In some cases, the leaf lamina is bistratose throughout (e.g. species in the Dicranaceae, Grimmiaceae, Pottiaceae, Fissidentaceae, Diphysciaceae, Amblystegiaceae and Vittiaceae). In other cases (e.g. species of Meesiaceae, Orthotrichaceae, Dicranaceae, Grimmiaceae, Pottiaceae, Amblystegiaceae, Ptychomitriaceae and Polytrichaceae) the lamina is unistratose basally and variously partly or exclusively bistratose in upper parts. Furthermore, species in several families (Grimmiaceae, Pottiaceae, Fissidentaceae, Brachytheciaceae, Hymenolomataceae, Orthotrichaceae, Amblystegiaceae and Neckeraceae) have bistratose streaks or patches along the lamina (Ireland and Schofield, 1967; Magill, 1976; Zander, 1976, 1986; Kramer, 1978; Ireland and Miller, 1982; Deguchi, 1983; Murray, 1984; Allen, 1988; Bellolio-Trucco and Ireland, 1990; Tan, 1990; Hedenäs, 1992; Bednarek-Ochyra and Ochyra, 1998, 2012; Ochyra and Vanderpoorten, 1999; Stech and Frahm, 2000; Casas *et al.*, 2001; Yip, 2002; Cano, 2003; Vanderpooten *et al.*, 2003; Gallego and Cano, 2007; Jimenez, 2007; Jimenez and Cano, 2008; Ochyra and Bednarek-Ochyra, 2011). These numerous occurrences, spanning a broad taxonomic range, indicate that a bistratose leaf lamina is also a homoplastic character, just like the tristichous condition. Thus, neither of these two prominent features of *Tricarinella* bears a clear taxonomic signal. It is, nevertheless, worth noting that the type of lamina seen in *Tricarinella* – entirely bistratose at the base and becoming increasingly unistratose apically, in a centripetal pattern – has no counterpart in the modern moss flora.

Compared with the tristichous condition and the bistratose lamina, costa anatomy is given more weight in moss taxonomy. While some features of costa anatomy are probably also homoplastic across the Bryophyta as a whole, many of them seem to provide support at lower taxonomic levels (Kawai, 1968; Schofield, 1985; Goffinet *et al.*, 2009). A homogenous costa, i.e. consisting of a single cell type, characterizes a number of moss families, among both the acrocarpous mosses (Meesiaceae, Orthotrichaceae, Rhabdoweisiaceae, Grimmiaceae, Seligeriaceae and Archidiaceae) and the pleurocarps (Superorder Hypnales, except Hypnodendrales) (Gradstein *et al.*, 2001; Frey and Stech, 2009; Goffinet *et al.*, 2009).

An important implication of the inferred upright, cushion-forming growth habit of *Tricarinella* is that this is an acrocarpous moss. Extant acrocarpous mosses with a homogeneous costa fall into two sub-classes of Class Bryopsida: Bryidae (Meesiaceae and Orthotrichaceae) and Dicranidae (Rhabdoweisiaceae, Grimmiaceae, Seligeriaceae and Archidiaceae). Among the Bryidae, the Meesiaceae compare well with *Tricarinella* (Table 1); the family even includes species with tristichous phyllotaxis (Gradstein *et al.*, 2001) and with leaves that exhibit a bistratose lamina (apically) (Deguchi, 1983), although the two features do not co-occur in the same species. However, the costa of the Meesiaceae consists of very small cells covered by an abaxial and adaxial epidermis of much larger cells (Ochyra *et al.*, 2008), very different from the large cells that form the costa of *Tricarinella*. This makes the Meesiaceae an unlikely taxonomic placement for *Tricarinella*.

The other acrocarpous homocostate Bryidae, the Orthotrichaceae, do not include tristichous species, but some species have a bistratose lamina apically or in patches (Zander, 1976). The Orthotrichaceae also lack a central strand (Gradstein *et al.*, 2001; Frey and Stech, 2009), which is a taxonomically important feature among mosses and rules them out as a possible taxonomic placement for *Tricarinella*. With both the Meesiaceae and Orthotrichaceae excluded, the homocostate acrocarpous Dicranidae provide the only potential taxonomic placement for *Tricarinella*.

Among homocostate acrocarpous Dicranidae, the Rhabdoweisiaceae and Archidiaceae do not include any species with a bistratose lamina of any kind or with tristichous phyllotaxis (Table 1). The Grimmiales include groups that share many features with *Tricarinella*. Of these, the Grimmiaceae and Seligeriaceae are homocostate. The Seligeriaceae only include a few species with bistratose leaf margins, and rarely display tristichous phyllotaxis (Vitt, 1976); additionally, Seligeriaceae are not known to produce gemmae. In contrast, many Grimmiaceae produce gemmae (Malcolm *et al.*, 2009; Ignatova and Muñoz, 2004) and include numerous representatives that feature different conformations of bistratose lamina (Ireland and Miller, 1982; Murray, 1984; Casas *et al.*, 2001; Cano, 2003; Ochyra and Bednarek-Ochyra, 2011; Bednarek-Ochyra and Ochyra, 1998, 2012), even though only few have tristichous phyllotaxis (Ignatova and Muñoz, 2004). Although both tristichous phyllotaxis and a bistratose lamina are homoplastic across mosses, as a group, we consider lamina bistratosity to bear a signal at lower taxonomic levels. In fact, according to Gradstein *et al.* (2001), in the Grimmiaceae, leaf anatomy provides nearly all the characters needed for identifying genera, if not species. Together

TABLE 1. *Comparison of* Tricarinella *with acrocarpous mosses with homogeneous costa*

Family	Sub-class, order	Tristichous phyllotaxis	Bistratose lamina	Central strand	Gemmae	Growth form
Tricarinella	–	+	+	+	?Axillary, leaf-borne	Cushion
Meesiaceae	Bryidae, Splachnales	+	+	+	–	Turf
Orthotrichaceae	Bryidae, Orthotrichales	–	+	–	Axillary, leaf-borne, rhizoidal	Cushion, etc.
Rhabdoweisiaceae	Dicranidae, Dicranales	–	–	+	Axillary, costa-borne	Cushion, turf
Archidiaceae	Dicranidae, Archidiales	–	–	+	–	Cushion, turf
Seligeriaceae	Dicranidae, Grimmiales	+	–	+	–	Turf
Grimmiaceae	Dicranidae, Grimmiales	+	+	+	Leaf-borne, costa-borne	Cushion, turf

Based on Bellolio-Trucco and Ireland (1990); Matteri and Ochyra (1999); Gradstein *et al.* (2001); Peralta and Vital (2006); Ochyra *et al.* (2008); Goffinet *et al.* (2009); and Frey and Stech (2009).

these make the Seligeriaceae an unlikely taxonomic placement for *Tricarinella* and support affinities with the Grimmiaceae. Particularly strong support for placement in the Grimmiaceae is also provided by the sinuous lamina cells of *Tricarinella*. Sinuous lamina cells are a valuable character routinely used to distinguish Grimmiaceae from other Dicranidae (e.g. Crum, 1983; Frey and Stech, 2009), thus increasing the robustness of our assignment of *Tricarinella* to this family. Nevertheless, as a set of morphological synapomorphies for the Grimmiaceae has yet to be defined (Streiff, 2005), it will be interesting to test the current placement of *Tricarinella* in this family, based strictly on a comparative approach, with cladistic analysis, as advocated for by Crepet *et al.* (2004).

Many species in family Grimmiaceae look similar to *Tricarinella* and share some of its features. For example, in the genus *Grimmia*, *G. capillata* De Not. and *G. torquata* exhibit three-ranked leaves, whereas *G. alpestris* (F. Weber & D. Mohr) Schleich. and *G. caespiticia* (Brid.) Jur. have leaves with bistratose portions (Ignatova and Muñoz, 2004). Gemmae similar to those of *Tricarinella* are seen in *G. torquata* Drumm., *G. muehlenbeckii* Schimp., *G. anomala* Hampe and *G. hartmanii* Schimp. (Ignatova and Muñoz, 2004). *Grimmia reflexidens* Müll. Hal. displays stem anatomy similar to that of *Tricarinella* (e.g. Ignatova and Muñoz, 2004) and so do species of other genera in the Grimmiaceae: *Guembella longirostris* (Hoole) Ochyra & Zamowiec, *Dryptodon fuscoluteus* (Hook.) Ochyra & Zamowiec and *Schistidium halinae* Ochyra (Ochyra *et al.*, 2008). Another species of *Schistidium* Bruch & Schimp., *S. deguchianum* Ochyra & Bednarek-Ochyra, has leaves with bistratose lamina (Ochyra and Bednarek-Ochyra, 2011). Leaves with bistratose portions of the lamina are also present in species of *Coscinodon* Spreng.: *C. cribrosus* (Hedw.) Spr. and *C. arctolimnius* (Steere) Steere (Hastings, 1999).

Considering these many similarities to diverse species of *Grimmia*, one would be tempted to place the Apple Bay moss in that genus. Favouring this assignment, *Grimmia* is a speciose genus that exhibits broad ranges of variation in many gametophyte characters among its numerous species (Lawton, 1971; Ignatova and Muñoz, 2004). However, the combination of tristichous phyllotaxis and a type of lamina bistratosity not documented in any other moss argue for placement of the Apple Bay moss in a new genus – *Tricarinella*. We consider this a more appropriate choice also pending discovery of the sporophytes of *Tricarinella*, which could contribute to refining the taxonomy of this moss.

Tricarinella *in the moss fossil record*

Tricarinella is currently the only pre-Cenozoic fossil representative of the Grimmiaceae, as well as one of very few unequivocal Dicranidae fossils known outside of amber deposits, and the only permineralized representative of the Grimmiaceae and Dicranidae. The Cenozoic fossil record of the Grimmiaceae is sparse, at best. A mention of *Grimmia subelongata* Goepp. et Menge in amber (Göppert, 1853; Dixon, 1927) lacks a description and illustration, and is considered invalid (Tropicos.org, Missouri Botanical Garden, May 1, 2017, www.tropicos.org). The only other report of fossil Grimmiaceae consists of a specimen described from Eocene Baltic amber as

Grimmia sp. (Frahm and Gröhn, 2013), but without an accompanying set of characters that unequivocally place that fossil in the genus. In contrast to the Grimmiaceae, other Dicranidae and especially Dicranaceae mark multiple occurrences in Baltic amber (Frahm, 2010). The rarity of Grimmiaceae in amber is unlikely to be due to human bias in their recognition. While acrocarpous mosses of uncertain taxonomic affiliation are present in amber (Frahm, 2010), these are unlikely to represent Grimmiaceae, because the latter, like the Dicranaceae, are relatively easily identified based on leaf morphology and anatomy as observed in amber-preserved specimens.

Britton and Hollick (1907) described moss compressions from Eocene shales of the Florissant Formation. The fossils were placed in the genus *Glyphomitrium* Brid. and discussed as similar to the Grimmiaceae (Britton and Hollick, 1907; Dixon, 1927). However, subsequent treatments have placed *Glyphomitrium* outside the Grimmiaceae and even the Dicranidae, in family Glyphomitriaceae of sub-order Bryidae (Tropicos.org, Missouri Botanical Garden, May 1, 2017, www.tropicos.org).

The oldest fossil compared with the Dicranidae is *Paleocampylopus buragoae*, a Permian moss based on compressions from the Russian Far East (Ignatov and Shcherbakov, 2009). *Paleocampylopus* is similar to the Dicranales in leaf morphology and the apical cup-shaped structures which, if they represent perigonia, compare well with those of *Campylopus*. However, the mode of preservation of *Paleocampylopus* does not allow for unequivocal assessment of whether those cup-shaped structures are perigonia or gemma cups. Other pre-Cenozoic fossils discussed as Dicranidae are the Triassic *Palaeosyrrhopodon* Ignatov et Shcherbakov (Ignatov and Shcherbakov, 2011), Jurassic *Ningchengia* Heinrichs, X. Wang, Ignatov et M. Krings (Heinrichs *et al.*, 2014) and the Cretaceous *Taimyrobryum* Ignatov, Heinrichs, Schäf.-Verw. et Perkovsky, compared with *Archidium* (Ignatov *et al.*, 2016).

The only unequivocal pre-Cenozoic member of the Dicranidae is *Campylopodium allonense* (Konopka *et al.*, 1998), a species based on charcoalified sporophytes from the Late Cretaceous (Santonian) of Georgia. Gametophytes associated with these sporophytes exhibit dicranaceous features and are hypothesized to be conspecific. The availability of numerous specimens, particularly taxonomically informative sporophytes, allowed for placement of these fossils in an extant genus of family Dicranaceae. Within this context it is worth noting that although represented by a single specimen, *Tricarinella* could be placed taxonomically down to the family level – Grimmiaceae – and in a distinct new genus. This highlights the resolving power of anatomically preserved specimens in the taxonomy of moss fossils.

Living environment of Tricarinella

We hypothesize that the absence of Grimmiaceae from amber, as discussed earlier, reflects taphonomic bias, as they occupy niches (saxicolous, terrestrial) that are less likely to contribute material to the amber taphonomic pathway, a pathway heavily biased toward the epiphytic components of the flora. This could be part of a broader pattern, whereby saxicolous species are rarely preserved in the fossil record, as proposed

by Gams (1932) and reiterated by Streiff (2005). The rarity of *Tricarinella*, represented by a single specimen in the rich and diverse bryophyte component of the Apple Bay flora, could be another reflection of this pattern, if *Tricarinella* was a saxicolous moss, like most other Grimmiaceae.

CONCLUSIONS

The Early Cretaceous moss, *Tricarinella crassiphylla* gen. et sp. nov., marks the oldest fossil records for both family Grimmiaceae and sub-class Dicranidae, providing a hard minimum age of 136 Ma for these groups. This is the fourth moss type formally described from the Valanginian Apple Bay flora of Vancouver Island and adds another component to the sparse pre-Cenozoic fossil record of mosses. The fact that this fossil could be placed taxonomically to the family and genus level, despite its diminutive size, re-emphasizes both the significance of gametophyte characters for moss taxonomy, even in the absence of sporophyte characters, and the considerable resolving power of anatomically preserved fossils, even when recovered from allochthonous assemblages deposited in marine sediments, like the flora from Apple Bay.

Tricarinella demonstrates additional anatomical and morphological diversity in the Grimmiaceae, a lineage with a fossil record consisting of a single potential data point and that, up until now, had no fossil record older than the Cenozoic. Discovery of *Tricarinella* emphasizes the importance of paleobotanical studies as the only approach allowing access to a significant segment of biodiversity, the extinct biodiversity, which is unattainable by other means of scientific investigation (Marshall, 2017). If extant biodiversity represents only a small fraction of all biodiversity that ever existed on Earth (Niklas, 1997; Marshall, 2017), then continued exploration of the fossil record is bound to reveal much more diversity of extinct mosses.

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