KRASSILOVIELLA LIMBELLOIDES GEN. ET SP. NOV.: ADDITIONAL DIVERSITY IN THE HYPNANAEAN MOSS FAMILY TRICOSTACEAE (VALANGINIAN, VANCOUVER ISLAND, BRITISH COLUMBIA)

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Premise of research.   Despite an increase in interest in the fossil record of bryophytes (i.e., liverworts, hornworts, and mosses), the biology and taxonomy of these organisms remain understudied and, at times, elusive. In the pre-Cenozoic, especially, few taxonomically informative moss fossils are known. From this perspective, the anatomically preserved Apple Bay flora of Vancouver Island holds a wealth of Cretaceous moss diversity that, until very recently, has remained unexplored.

Methodology.   Fossils are preserved anatomically in carbonate concretions and studied in serial sections prepared using the cellulose acetate peel technique.

Pivotal results.   Krassiloviella limbelloides gen. et sp. nov., defined by tricostate homocostate leaves and much-branched stems, is a new addition to the pleurocarpous moss family Tricostaceae (superorder Hypnanae).

Conclusions.   Krassiloviella limbelloides is the second bryophyte described as a result of ongoing studies of the Early Cretaceous Apple Bay flora of Vancouver Island. Krassiloviella is also the second genus of family Tricostaceae, which provides the oldest unequivocal evidence for the pleurocarpous superorder Hypnanae and a hard minimum age for the group. Revealing aspects of diversity unaccounted for in extant floras, such fossil bryophyte discoveries emphasize the importance of paleontology for efforts aimed at documenting the history of biodiversity.

Keywords: Cretaceous, fossil, Hypnanae, moss, permineralization, pleurocarpous.

Introduction

Embryophytes originated in the Early Paleozoic, more than 450 myr ago (Vavrdova 1990; Strother et al. 1996; Wellman et al. 2003; Rubinstein et al. 2010). However, the oldest unequivocal moss fossils are Early Carboniferous, ca. 330 myr old (Hübers and Kerp 2012). Subsequently, diversification in the group gave rise to several easily recognized major lineages (e.g., sphagnalean, polytrichalean, dicranalean, and pleurocarpous mosses), and today there are more than 13,000 described moss species (Goffinet et al. 2009). Despite the long fossil record and significant levels of extant diversity, the moss fossil record is relatively sparse. Importantly, whereas mosses are relatively well represented in the Cenozoic record, with several fossils representing extant lineages (many of which are known from amber deposits; Taylor et al. 2009),

only about 70 moss species have been reported from pre-Cenozoic deposits. These represent a minute fraction of overall moss diversity, and many of the fossil species are too incompletely understood to be placed into a modern taxonomic framework (e.g., Oostendorp 1987; Ignatov 1990; Taylor et al. 2009).

Most fossil mosses are preserved as compressions, while anatomical preservation is rare, especially in pre-Cenozoic deposits (e.g., Taylor et al. 2009). Aside from the moss described here, anatomical preservation is rare among fossil mosses and includes cuticular preservation (Hübers and Kerp 2012), permineralization (Smoot and Taylor 1986; Shelton et al. 2015), preservation in amber (e.g., Hedenäs et al. 2014), and charcoalification (Konopka et al. 1997, 1998).

Throughout the Mesozoic, a few fossils have been compared to pleurocarpous mosses, a group of mosses with typically much-branched stems and sporophytes borne on short specialized branches. Most notable among these are *Palaeodichelyma* Ignatov et Shcherbakov; *Bryokhutuliinia* Ignatov; *Vetiplanaxis* N.E. Bell; *Tricosta* Shelton, Stockey, Rothwell et Tomescu; and *Uskatia* Neuburg (Oostendorp 1987;

Ignatov and Shcherbakov 2007, 2011a; Ignatov et al. 2011; Hedenäs et al. 2014; Shelton et al. 2015). The Early Cretaceous moss described here adds to the sparse record of pre-Cenozoic anatomically preserved mosses. Comparisons with extinct and extant mosses indicate that this plant represents a new genus and species, *Krassiloviella limbelloides*, within the extinct pleurocarpous family Tricostaceae. This moss provides another example of the unique tricostate condition once widespread in the Northern Hemisphere during the Mesozoic and adds to the earliest fossil record of pleurocarpous mosses.

Material and Methods

At least 20 gametophytes are preserved by cellular permineralization in more than 15 calcium carbonate concretions, as part of an allochthonous fossil assemblage deposited in nearshore marine sediments. The concretions are included in graywacke beds exposed on the northern shore of Apple Bay, Quatsino Sound, on the west side of Vancouver Island, British Columbia, Canada (lat. 50°36′21″N, long. 127°39′25″W; UTM 9U WG 951068). Layers containing the concretions 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, personal communication, 2013).

The Early Cretaceous Apple Bay flora includes lycophytes (Stockey 2004), equisetophytes (Stanich et al. 2009), at least 10 fern families (Smith et al. 2003; Hernandez-Castillo et al. 2006; Little et al. 2006a, 2006b; Rothwell and Stockey 2006; Stockey et al. 2006; Vavrek et al. 2006; Rothwell et al. 2014), numerous gymnosperms (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, 2014b; 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 more than 20 distinct moss morphotypes currently recognized (Tomescu et al. 2012; Shelton et al. 2015). Pleurocarpous, polytrichaceous, and leucobryaceous mosses are present, as well as several morphotypes of unknown affinities, including at least two other distinct tricostate types.

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. Images were processed using Photoshop (Adobe, San Jose, CA). All specimens and preparations are housed in the University of Alberta Paleobotanical Collections (UAPC-ALTA), Edmonton, Alberta, Canada.

Terminology. 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.

Systematics

Class—Bryopsida Rothm.

Subclass—Bryidae Engl.

Superorder—Hypnanae W.R. Buck, Goffinet et A.J. Shaw

Order—incertae sedis

Family—Tricostaceae Shelton, Stockey, Rothwell et Tomescu

Emended family diagnosis. Gametophyte plants pleurocarpous. Stems regularly to irregularly pinnately branched; central conducting strand absent. Cortical cells thin walled; hyalodermis or thick-walled outer cortex lacking. Paraphyllia absent. Leaves helically arranged, with three costae (tricostate). Laminal cells isodiametric to elongate. Alar regions inconspicuous to well differentiated. Gametangia one to few, borne on lateral specialized (perigonial, perichaetial) shoots.

Genus—Krassiloviella Shelton, Stockey, Rothwell et Tomescu, gen. nov.

Generic diagnosis. Gametophytes solitary or in tufts. Stems terete. Cortical cells similar in size across stem and with evenly thickened walls. Rhizoids present in basal regions of shoots. Shoots isophyllous. Leaves erect, straight, symmetrical, tricostate. Costae very strong, arising separately; lateral costae thinner than central costa. Distinct epidermis on both ab- and adaxial surface of costae; costae otherwise homogeneous. Alar regions minute, weakly differentiated. Laminal cells smooth, thin walled; in leaf base slightly elongate, inflated with oblong, oval, irregular, or isodiametric shapes; laminal cells above leaf base quadrate to isodiametric. Sporophytes unknown.

Etymology. *Krassiloviella*, after the late Dr. Valentin A. Krassilov, for his contributions to Mesozoic floras that include treatments of numerous fossil bryophytes. It was Dr. Krassilov's keen eye that first detected the tricostate condition in fossil mosses from eastern Russia.

Type Species—Krassiloviella limbelloides Shelton, Stockey, Rothwell et Tomescu, sp. nov.

Specific diagnosis. Gametophyte branching irregular to pinnate, complanate, concentrated distally along main stems. Branches at regular intervals (1–4 mm) at angles of 25°–45°. Stems 350–450 μm in diameter; epidermis distinct, consisting of smaller cells. Rhizoids smooth walled, 12–14 μm diameter; some rhizoids present on leaves. Leaves densely spaced, 4.5–6/mm, with 3/8 helical phyllotaxis, diverging from stem at 5°–20° angles. Leaves lanceolate, concave throughout, up to 5 mm long and 0.9 mm wide. Leaf margin plane or slightly curved adaxially (incurved), entire or minutely dentate. Leaf apex acute to apiculate. Lamina up to three cells thick between costae in leaf apex; elsewhere, lamina unistratose. Leaf margin six to 10 cells wide in basal half of leaf, tapering to

one cell wide in apex. Costae parallel with leaf margin, percurrent, converging in apex; composed of thin-walled cells. Costae 50–80 μm thick. Median costa 12–16 cells wide (125–90 μm wide from leaf base to apex), ca. seven cells thick. Lateral costae ca. eight cells wide (80–70 μm wide from leaf base to apex), five to seven cells thick. Costal cells 30–100 μm long, 5–10 μm in diameter; epidermal cells of costae transversely elongate or isodiametric, 10–12 μm. Alar regions poorly differentiated, consisting of ca. 25–50 cells. Lamina cells at leaf base elongated, length-to-width ratio up to 4:1, 12–24 μm (up to 40 μm) long, 12–16 μm wide; above base, lamina cells up to 1.33:1, 8–10 μm, forming longitudinal files. Juxtacostal cells larger than other lamina cells.

Holotype hic designatus. Gametophyte shoot in rock slabs UAPC-ALTA P17596 C bot and D (figs. 1*A*, 2*C*, 3*D*, 4*A*–4*D*, 4*G*, 5*E*, 5*F*, 6*A*, 7*D*–7*F*, 8*C*, 8*E*, 9*D*, 9*E*).

Paratypes. UAPC-ALTA P25 B bot (figs. 1*B*, 2*A*, 2*B*, 3*A*–3*C*, 3*E*, 4*G*, 5*D*, 7*G*–7*I*, 8*D*, 10*A*–10*K*, 11*A*, 11*B*), P13131 D bot (figs. 6*B*–6*F*, 7*A*–7*C*, 8*A*, 8*B*, 9*A*–9*C*), P15388 A (fig. 4*E*), P17345 C top (fig. 5*A*–5*C*).

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

Stratigraphic occurrence. Longarm Formation equivalent.

Age. Valanginian (ca. 136 Ma), Early Cretaceous.

Etymology. Specific epithet *limbelloides* for the overall similarity in leaf morphology with species of the genus *Limbella* Müll. Hal. (Amblystegiaceae).
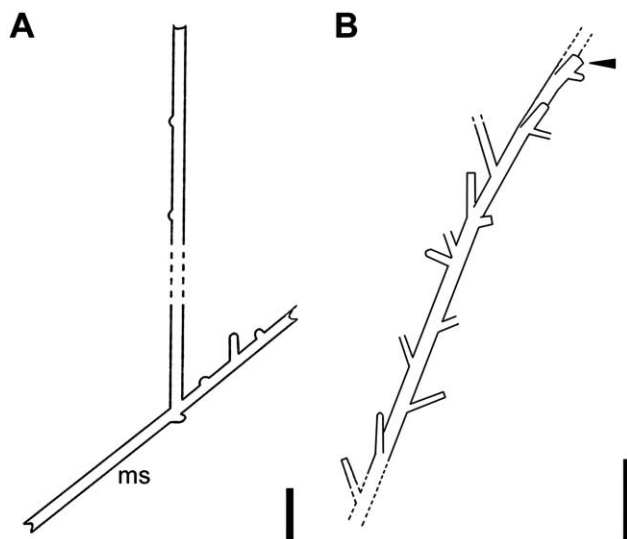
Fig. 1 Branching architecture of *Krassiloviella limbelloides* gen. et sp. nov. *A*, Reconstruction showing the main stem (ms) with a missing tip and the long, reiterative stem with a missing tip (*top*); note that the branching along the main stem is restricted to the distal portion; dashed lines represent portions of the stem missing in between slabs. P17596 C bot #1-#68 and P17596 D #1-#45. *B*, Reconstruction with the main stem bearing a putative gametangial branch (arrowhead) directly subtended by a short, narrow branch; dashed lines represent portions of the stem removed by saw cut; P25 B bot #1b-#73b. Scale bars = 2 mm.

Description

Habit, Branching, Shoot Architecture, and Stem Anatomy

Krassiloviella limbelloides is represented by more than 20 gametophyte shoots. Sporophytes have not been found. The gametophytes are solitary or occur in tufts and are at least 2 cm long. Branching of *K. limbelloides* occurs at regular intervals (the length of which varies between specimens; 0.8–4.0 mm) and at 25°–45° angles (fig. 3*A*–3*C*). Reconstructions of two extensive specimens based on serial sections (fig. 1*A*, 1*B*) show irregularly to pinnately branched gametophyte stems with mostly complanate branching (as determined based on serial sections that show lateral branches and branch primordia diverging in approximately the same plane from the main stems). One of these specimens is at least 10.5 mm long (figs. 1*A*, 4*A*–4*C*), unbranched in the proximal 6 mm, and with branches arising in the distal 4.5 mm. A well-developed reiterative stem 12 mm long diverges 4 mm from the distal end of the main stem (the tip of the main stem is not preserved; fig. 1*A*). The reiterative stem bears only two minute ($\leq$100-μm-long) branches, but its tip is missing (figs. 1*A*, 4*A*–4*D*). Another extensive specimen (figs. 1*B*, 3*A*–3*C*, 10*A*), at least 11 mm long, is branched throughout, with at least one lateral demonstrating second-order branching. Stems are terete, 370–430 μm in diameter, and ca. 25 cells across and lack a central conducting strand (fig. 2*A*). Cortical cells are round to polygonal in transverse sections and 60–140 μm long and have the same diameter (11.5–18.5 μm) across the stem. Their walls are evenly thin (<1 μm), with end walls that are oblique or tapered (fig. 2*B*). The well-defined epidermis consists of darker cells with rectangular shapes 9–14 μm thick, 11.5–16 μm wide, and 9–17 μm tall and slightly thicker walls (figs. 2*C*, 3*D*).

Branches are 0.3–1.0 mm long, 150–235 μm wide, and <15 cells across (fig. 3*A*–3*C*, 3*E*) and are composed of mostly short, inflated cells. Most branch tips are incompletely preserved due to taphonomy and diagenesis (e.g., abrasion during transport and tips replaced by crystals; fig. 4*F*), sometimes possibly as a result of truncation by herbivores (fig. 4*A*, 4*D*; see "Discussion") or simply because of lower preservation potential of delicate apical meristematic regions. Truncated distal ends have a characteristically concave outline, with the outermost one to a few layers of cells darkened. Leaves adjacent to the truncated tips conform to the same concave shape and bear dark cells distally; this is consistent with an herbivore having removed the entire shoot tip (fig. 4*A*, 4*D*).

Leaves are isophyllous, follow a 3/8 phyllotaxis with imbricate arrangement (as determined by observation of serial sections), and densely cover the stems (4.5–6 leaves/mm; e.g., figs. 3*A*–3*C*, 4*A*, 4*E*). Leaves are straight (or rarely recurved; fig. 4*B*) and diverge from the stems at angles of 5°–20°, with wider angles where leaves subtend branches (fig. 4*C*). In one longitudinal section, a short branch (<1 mm long) bears leaves <3 mm long that are erect or delicate and contorted (fig. 4*G*). However, leaves on most branches are similar to stem leaves, albeit slightly smaller. Paraphyllia have not been observed.
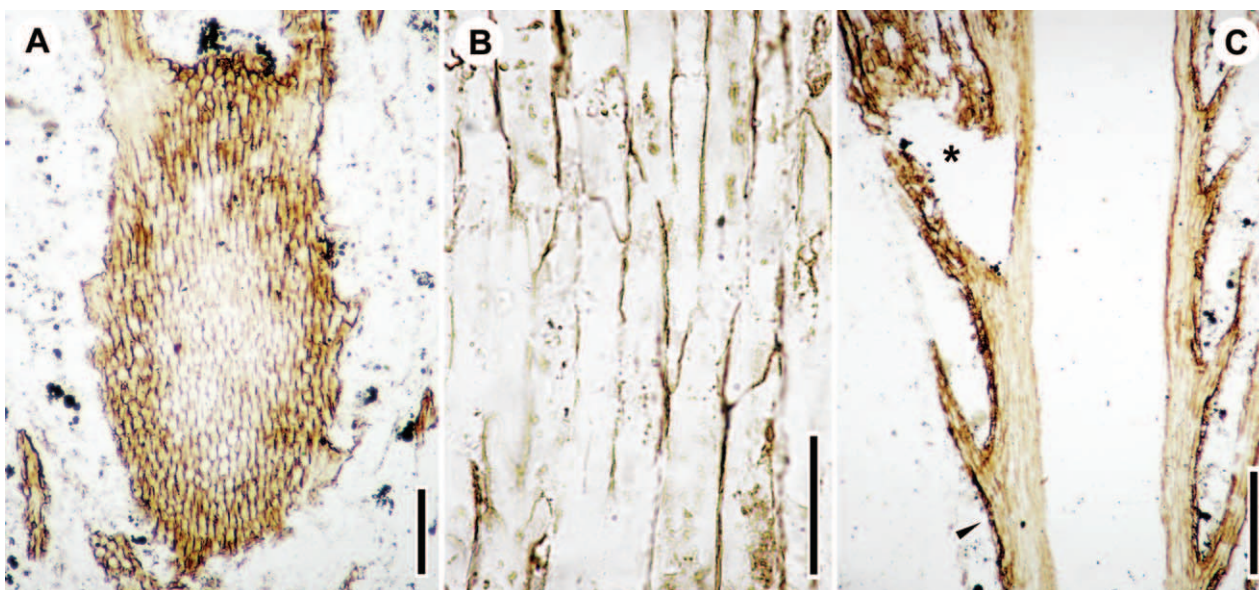
Fig. 2 Stem anatomy of *Krassiloviella limbelloides* gen. et sp. nov. *A*, Oblique section of the stem showing the arrangement of the cortical cells and the absence of the conducting strand; note that the epidermis is not preserved. Scale bar = 100 μm. P25 B bot #8b. *B*, Cortical cells in longitudinal section showing thin walls and tapered end walls. Scale bar = 30 μm. P25 B bot #13b. *C*, Longitudinal section of the stem showing a well-defined epidermis of dark cells (arrowhead) and a minute lateral branch (asterisk); note that most of the cortex in the stem and branch is not preserved. Scale bars = 200 μm. P17596 C bot #51.

One gametophyte base bears dense multicellular rhizoids (fig. 5A–5C) that are 12–14 μm in diameter and smooth walled and have oblique end walls (fig. 5C). In addition to stems, rhizoids are found attached to leaves near the leaf base either abaxially (fig. 5B) or adaxially (fig. 5D). In one paradermal section, rhizoids are attached to leaf tissue away from the leaf base (fig. 5E, 5F), but it is unclear whether they are attached to the lamina or the costae due to incomplete preservation.

Leaf Morphology and Anatomy

The leaves of *K. limbelloides* are symmetrical, lanceolate, and concave throughout and are broadly attached to the stems (figs. 6, 7C, 7I). They are up to 5 mm long and 0.9 mm wide (ca. 500 μm wide at the base; fig. 6A). Margins are plane or slightly incurred (figs. 6, 7C, 8B) and entire or with minute dentition near the leaf tip (fig. 7G). Leaf apices are acute and apiculate (fig. 7G).

Leaves are tricostate, with a unistratose lamina through most of the leaf length (e.g., fig. 6). Laminae are delicate, as evidenced by their typically incomplete preservation (e.g., figs. 4E, 6, 7C). Where unistratose, the lamina is 11.5–14 μm thick. However, the lamina is bistratose or tristratose in areas where costae converge at the leaf apex (fig. 7A, 7C). The three costae arise separately (fig. 7H, 7I). The lateral costae run parallel to the leaf margin and converge well into the apex (thus, all three costae are percurrent; figs. 6, 7A, 7C). The leaf margin is six to 10 cells wide in the basal half of the leaf, four to six cells wide at midleaf, and one cell wide in the apex. At

the widest point of the leaf, the lamina is 15 cells wide between the median and the lateral costae (fig. 6).

The median costa is 95–125 μm wide in the lower half of the leaf and 70–90 μm wide in the apex; lateral costae are 50–80 μm wide, becoming 35–70 μm wide in the apex (e.g., figs. 6B–6F, 7A–7C, 7F). The median costa is 12–16 cells wide and ca. seven cells thick (e.g., fig. 9B), whereas lateral costae are eight cells wide and five to seven cells thick (e.g., fig. 8C). Costae are 50–80 μm thick and have a 6–10-μm-thick epidermis on both the ab- and the adaxial surfaces (fig. 7D, 7E, 7H, 7I). The cells of this epidermis are isodiametric or slightly elongated transversely and are 5–12 μm across. The middle layers of the costae are homogeneous, composed of thin-walled cells (ca. 1 μm thick; figs. 8B, 8C, 9B). In longitudinal sections, costal cells are 70–100 μm long proximally and 30–50 μm long distally, mostly 5–10 μm in diameter, and tapered at one or both ends (fig. 8A).

Cells of the lamina are smooth and thin walled (ca. 1 μm thick; figs. 8D, 8E, 9A, 9C–9E). In the leaf base, lamina cells have 2–2.5∶1 length-to-width ratios (up to 4∶1 in leaves of specialized branches) with mostly oval shapes 12–40 μm long and 12–16 μm wide (fig. 8D, 8E). Alar regions are small, weakly differentiated, and incompletely preserved (fig. 9A); they consist of 25–50 cells, with morphology comparable to other cells in the leaf base. Above the base, laminal cells form longitudinal files of mostly isodiametric or oval-shaped cells (up to 1.33∶1) 8–10 μm in diameter (up to 18 μm long; figs. 7F, 9C–9E). One or two rows of larger cells 14–35 μm long and 25 μm wide occupy juxtacostal positions (figs. 7F, 9D, 9E).
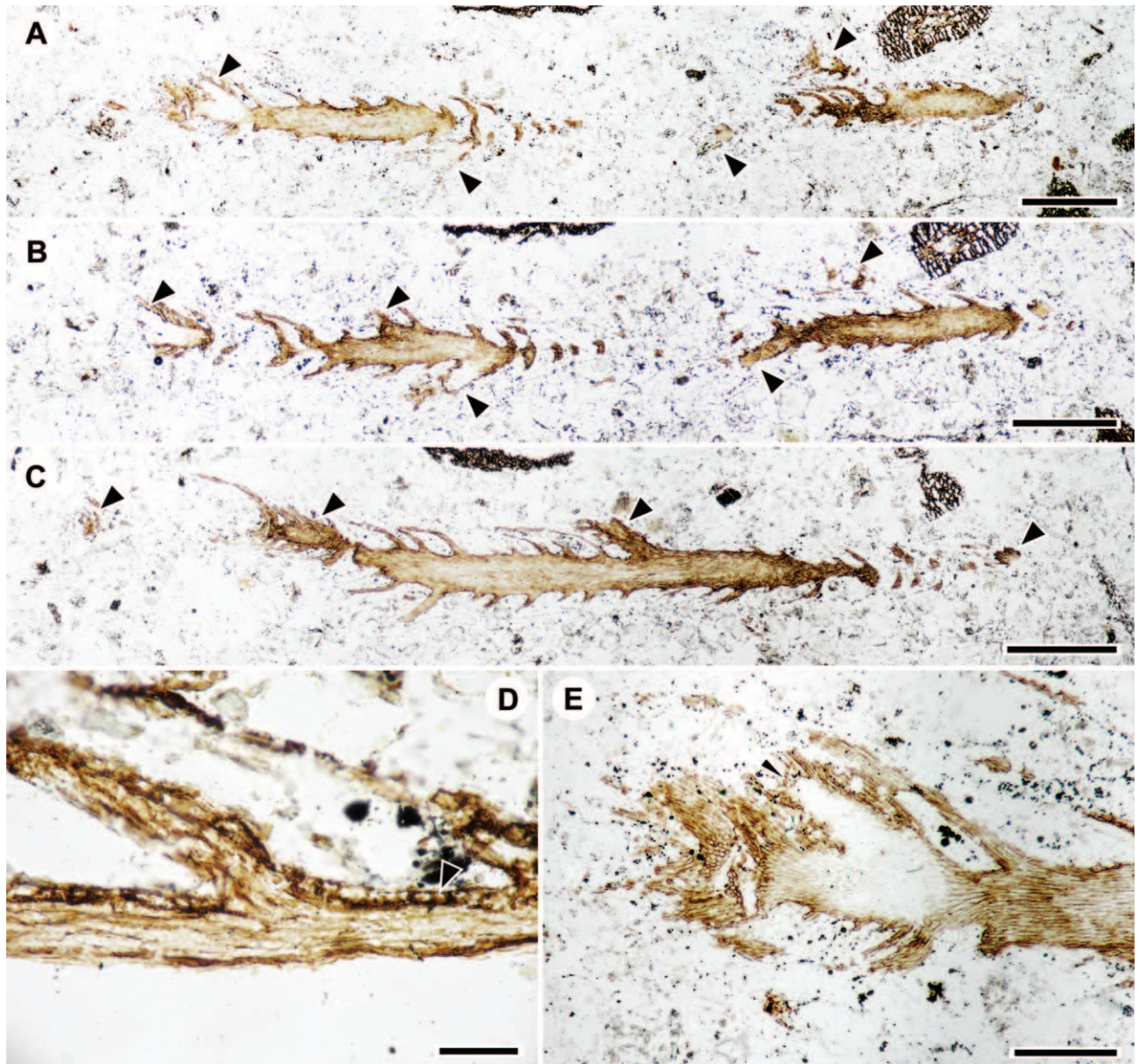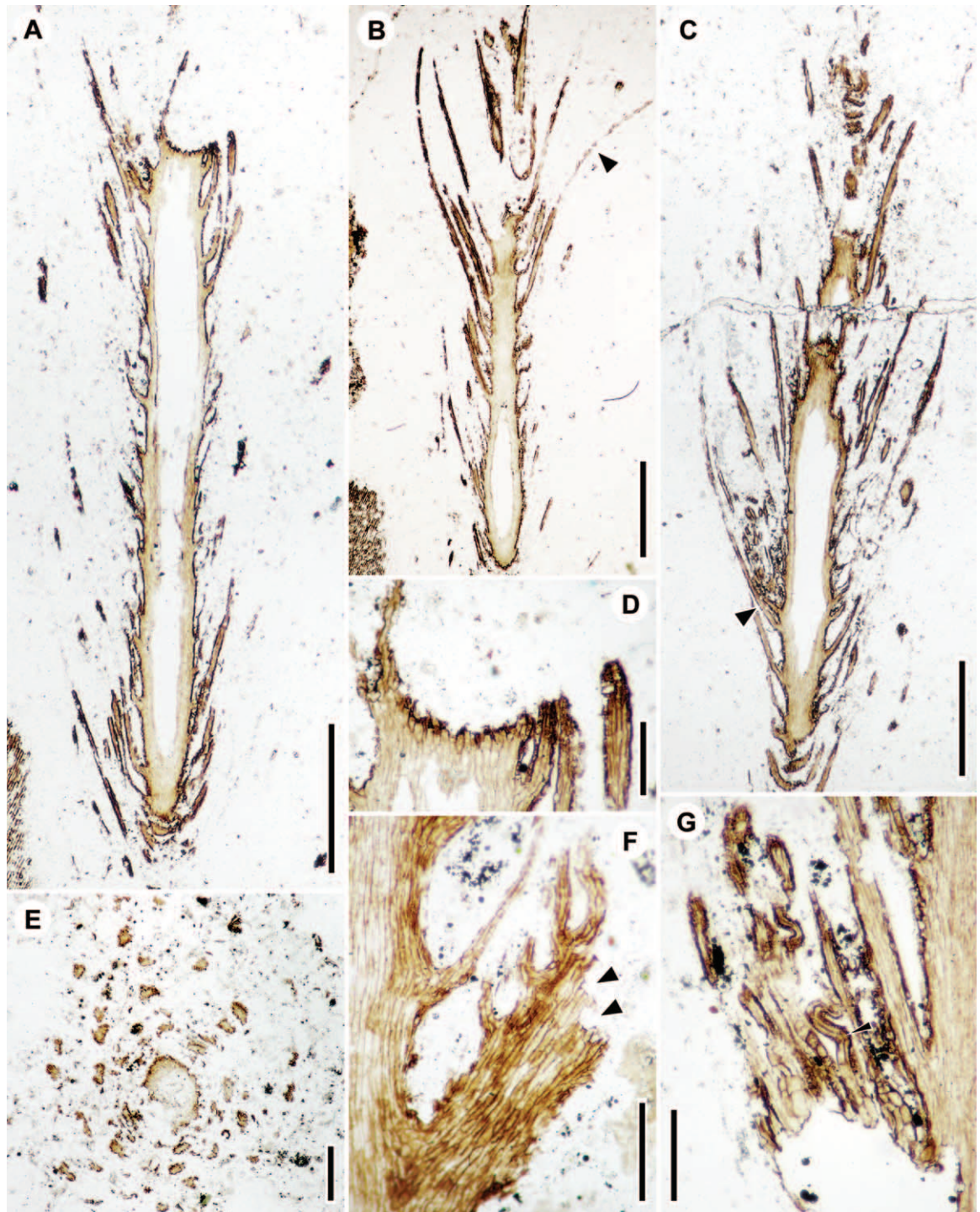
Fig. 3 Shoot architecture of *Krassiloviella limbelloides* gen. et sp. nov. *A–C*, Shoots in longitudinal section showing branches (arrowheads) and numerous leaf bases. Scale bars = 1 mm. P25 B bot #27b, P25 B bot #30b, P25 B bot #41b. *D*, Stem in longitudinal section showing the epidermis (arrowhead) composed of rectangular cells; most cortex is not preserved (*bottom*). Scale bar = 50 μm. P17596 C bot #51. *E*, Shoot in longitudinal section showing the entire branch tip (arrowhead). Scale bar = 300 μm. P25 B bot #27b.

Specialized Branch

One specimen bears a bud-like (gametangial?) lateral branch (figs. 1*B*, 10) directly subtended by a narrow vegetative lateral branch 300 μm long and 150 μm in diameter (figs. 1*B*, 10*A*). Several other short lateral branches are borne on this specimen, but none is bud-like. The bud-like branch is a thick axis ca. 250 μm across and 250 μm long with densely arranged, erect leaves (innermost leaves <2 mm long; cells in the leaf base elongate, up to 4:1; fig. 10*C*). The shoot tip is expanded and slightly bulging and bears the darkened bases of at least

five incompletely preserved structures (e.g., figs. 10*B*, 10*D*, 11) and delicate leaf bases surrounding them (fig. 10*B*, 10*D*). The base of the structures is ca. 50 μm wide, eight cells across, and five cells high (e.g., fig. 11). A delicate, incompletely preserved tissue (gametangia?) occupies the area above the bases (e.g., figs. 10*B*, 10*D*, 11). Attached to one of these bases, a column of delicate tissue suggests an archegonium (fig. 11). At the periphery of the shoot tip, an incompletely preserved, dark cellular body ca. 55 μm long and 42 μm wide (six cells long and four cells wide) may represent a developing embryo (fig. 11). At least one uniseriate paraphysis is also

Fig. 4 Shoot architecture of *Krassiloviella limbelloides* gen. et sp. nov. *A*, Shoot longitudinal section showing several leaf bases and an incomplete tip. Scale bar = 1 mm. P17596 D #37. *B*, Shoot longitudinal section showing several leaf bases and leaf divergence angles. Arrowhead = recurved leaf. Scale bar = 1 mm. P17596 D #30. *C*, Shoot in longitudinal section showing erect, densely arranged leaves; note the slightly wider divergence angle of the leaf subtending branch (arrowhead). Scale bar = 1 mm. P17596 C bot #45. *D*, Detail of *A* showing a concave shape to the remaining tip (suggesting herbivory); note the darkened outer cell layers of the stem tip and adjacent leaves. Scale bar = 150 μm. P17596 D #37. *E*, Shoot cross section showing helically arranged, overlapping leaves and characteristic incomplete preservation of laminae. Scale bar = 300 μm. P15388 A #23. *F*, Branch with the tip removed by taphonomic processes; note the crystalline structures at the remaining branch tip (arrowheads). Scale bar = 200 μm. P25 B bot #41b. *G*, Branch with an entire tip and short, delicate leaves; note at least one contorted leaf base (arrowhead). Scale bar = 150 μm. P17596 C bot #53.
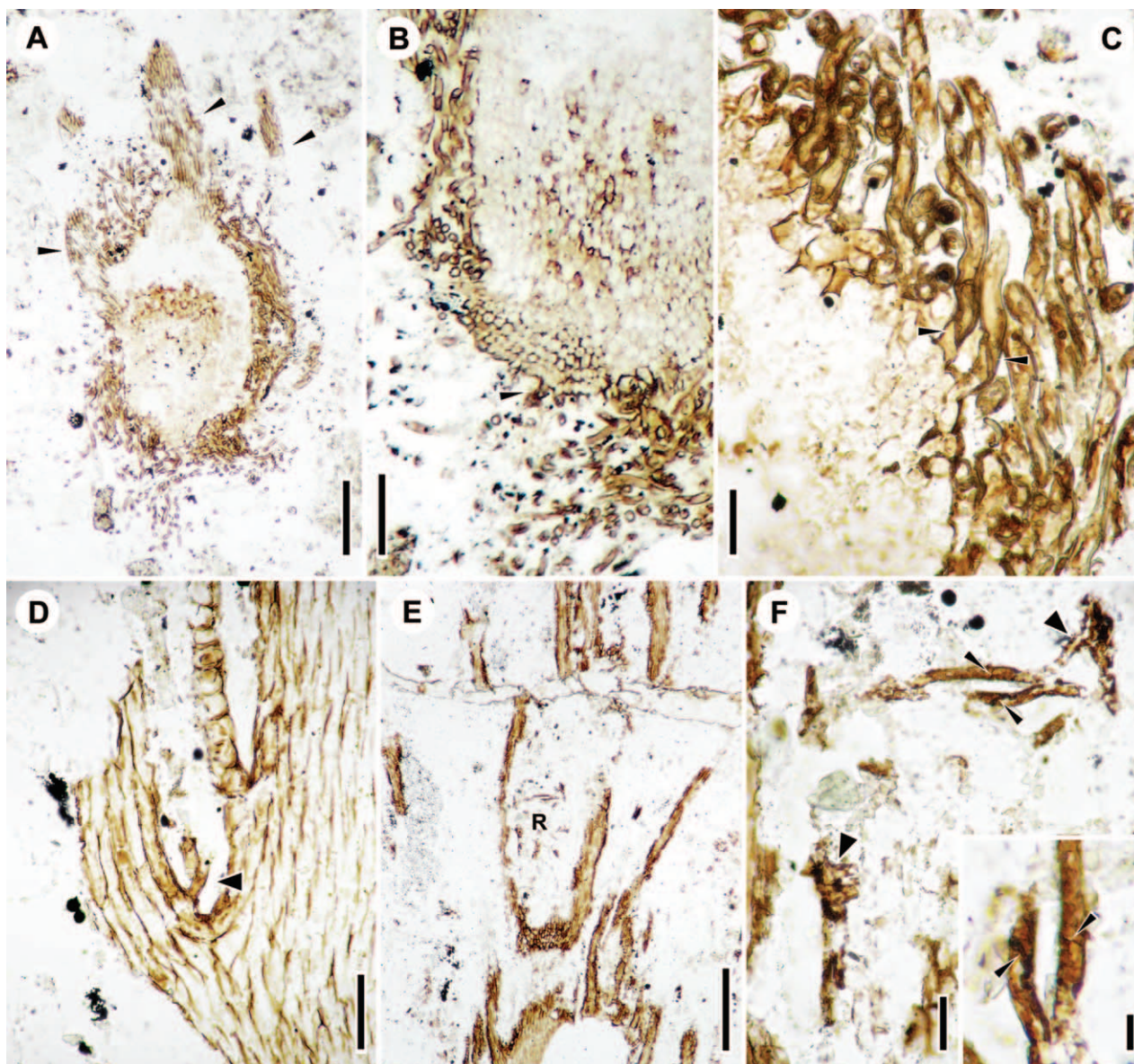
Fig. 5   Rhizoids of *Krassiloviella limbelloides* gen. et sp. nov. *A*, Transverse section of the gametophyte base showing dense rhizoids; note the three costa bases of a single leaf (arrowheads). Scale bar = 200 μm. P17345 C top #18a. *B*, Transverse section of the gametophyte base showing dense rhizoids attached to the stem; few rhizoids are attached to the abaxial surface of the central costa (arrowhead). Scale bar = 100 μm. P17345 C top #14a. *C*, Detail of *A* showing smooth-walled rhizoids with oblique end walls (arrowheads). Scale bar = 50 μm. P17345 C top #18a. *D*, Leaf axil in longitudinal section showing the rhizoid base (arrowhead) attached to the adaxial surface of the costa. Scale bar = 50 μm. P25 B bot #12b. *E*, Paradermal section of incompletely preserved leaf showing few rhizoids (R) attached to the leaf surface. Scale bar = 300 μm. P17596 C bot #51. *F*, Detail of *E* showing rhizoid bases (thick arrowheads) and oblique end walls (thin arrowheads; *inset*). Scale bars: *A–F* = 30 μm; *inset* = 10 μm. P17596 C bot #51.

preserved, consisting of cells ca. 36 μm long and 15 μm thick (fig. 10*D*).

Discussion

The Tricostate Condition

The tricostate condition, in which three costae originate separately at the leaf base, is known only in pre-Cenozoic fossil mosses (i.e., *Tricostium* Krassilov; *Tricosta* Shelton, Stockey, Rothwell et Tomescu; and now *Krassiloviella*) and clearly sets these plants apart from all other living and extinct mosses (Krassilov 1973; Ignatov and Shcherbakov 2011*a*, 2011*b*; Shelton et al. 2015). Few extant mosses possess leaf features similar to the lateral costae of a tricostate moss. These include, but are not limited to, multistratose thickenings of the lamina in some species of *Coscinodon* Spreng. (Grimmiaceae; Hastings and Deguchi 1997) and *Scouleria* Hook. (Scouleriaceae;
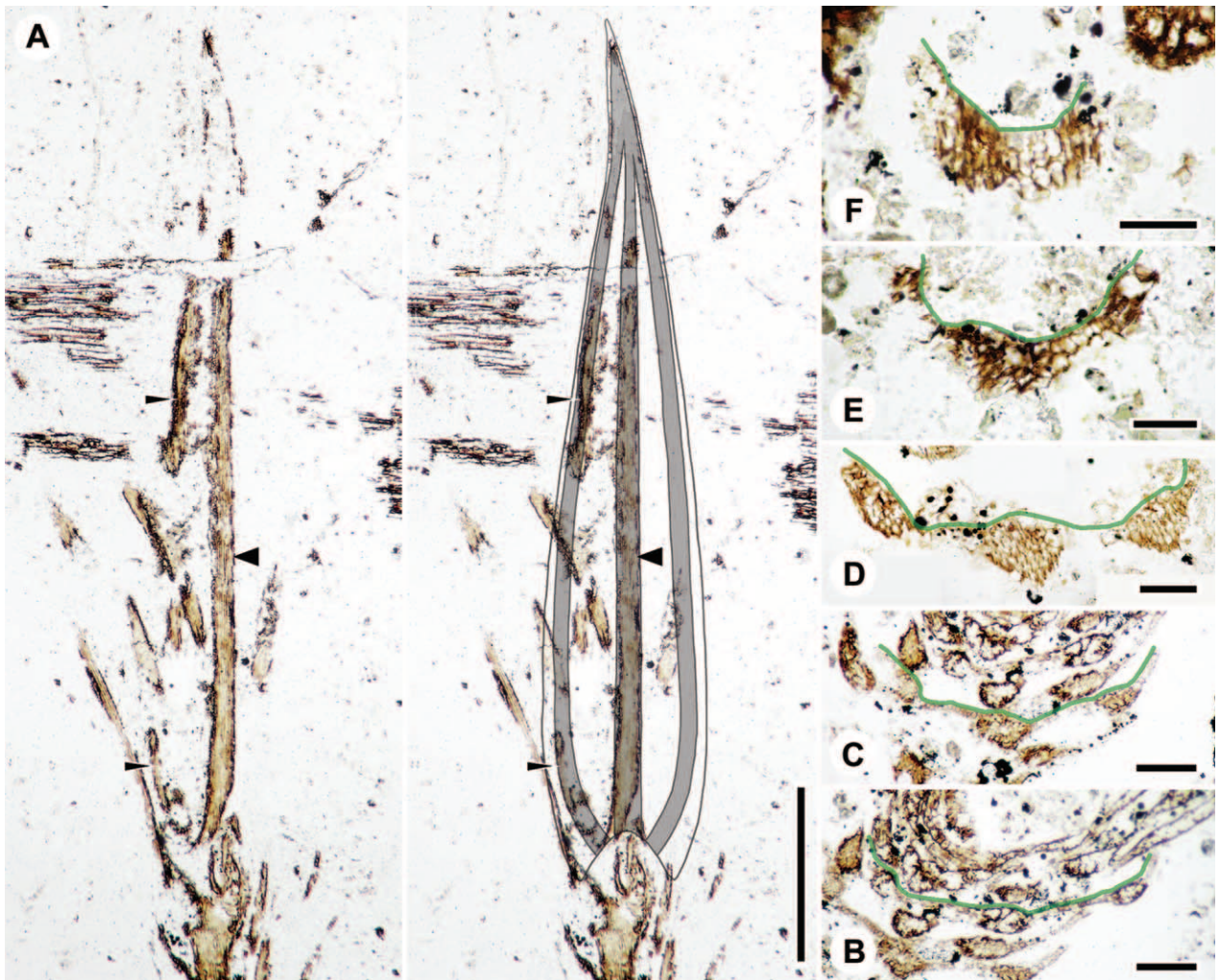
Fig. 6 Leaf anatomy and morphology of *Krassiloviella limbelloides* gen. et sp. nov. *A*, Paradermal section showing the entire leaf length; thick arrowheads indicate the central costa; thin arrowheads indicate the left lateral costa (the right lateral costa is not shown); at right, the leaf model is superimposed over the same image. Scale bar = 1 mm. P17596 C bot #66. *B–F*, Series of leaf transverse sections from near the base (*B*) to the apex (*F*); leaves are traced adaxially. Scale bars: *B–D* = 100 μm; *E, F* = 50 μm. B, C: P13131 D bot #17c. *D*: P13131 D bot #10c. *E*: P13131 D bot #63c. *F*: P13131 D bot #49c.

Matteri 1979; Churchill 1985; Carter at al. 2014; Ignatova et al. 2015), as well as intramarginal limbidia in *Limbella tricostata* Bartr. (Amblystegiaceae; Lawton 1971) and some species of *Calymperes* Sw. (Calymperaceae) and *Teniolophora* W.D. Reese (Pottiaceae; Gradstein et al. 2001). Only in *Limbella* Müll. Hal. is the anatomy of these lateral accessory structures (limbidia) closely comparable to that of the costa (Lawton 1971). While these structures of *Limbella* are the best modern analogs to the lateral costae of extinct tricostate mosses, their marginal position suggests a different developmental pathway from costae (Goffinet et al. 2009). Differences in the stem conducting strand, leaf length, and costal anatomy also distinguish *Limbella* from *Krassiloviella limbelloides*. Thus, overall, extant moss diversity does not include any structures equivalent to the lateral costae of tricostate mosses (Shelton et al. 2015).

Generic Placement

Mosses that share the tricostate condition include the genus *Tricostium*, with three species reported from Mesozoic (Triassic to Early Cretaceous) and possibly Permian rocks in Russia and Mongolia (Krassilov 1973; Ignatov and Shcherbakov 2011*a*, 2011*b*), and *Tricosta plicata*, described from the same Apple Bay locality on Vancouver Island as *Krassiloviella* (Shelton et al. 2015; table 1). Although both *Tricostium* and *Tricosta* possess tricostate leaves, disparity in preservation and the type and number of characters available leads to differences in taxonomic status. Namely, whereas genus *Tricostium* is based on leaf compressions that preserve little anatomical detail (and, as such, corresponds to an organ-genus or a morphogenus; Greuter et al. 2000), *T. plicata* is represented by numerous
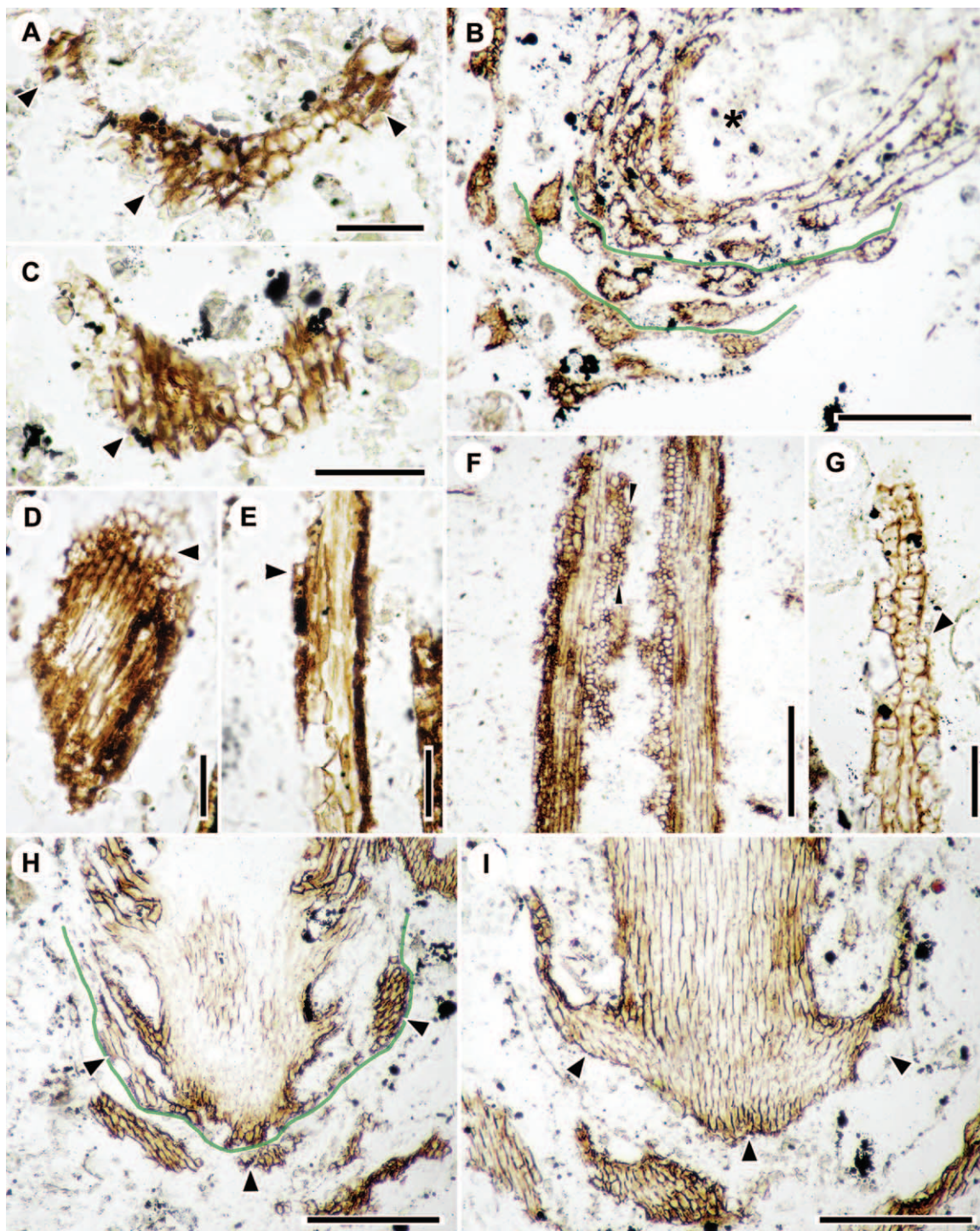
Fig. 7 Leaf anatomy of *Krassiloviella limbelloides* gen. et sp. nov. *A*, Leaf tip transverse section below level where one lateral costa (*left*) merges with the central costa; arrowheads indicate three costae; lamina is bistratose in between central and right lateral costae. P13131 D bot #63c. *B*, Transverse section of shoot showing tricostate, concave leaves with plane margins (two leaves traced adaxially); the asterisk represents the center of the incompletely preserved stem. P13131 D bot #17c. *C*, Leaf tip transverse section above level where one lateral costa (*left* in *A*) merged with the central costa (arrowhead); the lamina is bi- or tristratose in between central and right lateral costae. P13131 D bot #49c. *D*, Leaf costa in oblique section showing more or less face view of epidermis (arrowhead). P17596 C bot #47. *E*, Leaf costa in longitudinal section showing small rectangular cells of the epidermis (e.g., arrowhead). P17596 C bot #44. *F*, Paradermal section of the leaf showing the central costa (*right*), the lateral costa (*left*), and the laminal cells forming longitudinal files (in between arrowheads); larger juxtacostal cells are adjacent to the costae. P17596 C bot #66. *G*, Apiculate leaf tip (apiculus) in paradermal section; note the minute dentition (arrowhead). P25 B bot #1b. *H*, Oblique section of the stem showing the leaf base (traced abaxially) just above the point of divergence of the lateral costae (left and right arrowheads); the central costa (arrowhead at bottom) is incompletely preserved and attached to the stem. P25 B bot #2b. *I*, Oblique section of the shoot showing the leaf base below the point of divergence; arrowheads indicate the positions of the costae. P25 B bot #2b. Scale bars: *A, B, D, E, G* = 50 μm; *C, F, H, I* = 200 μm.
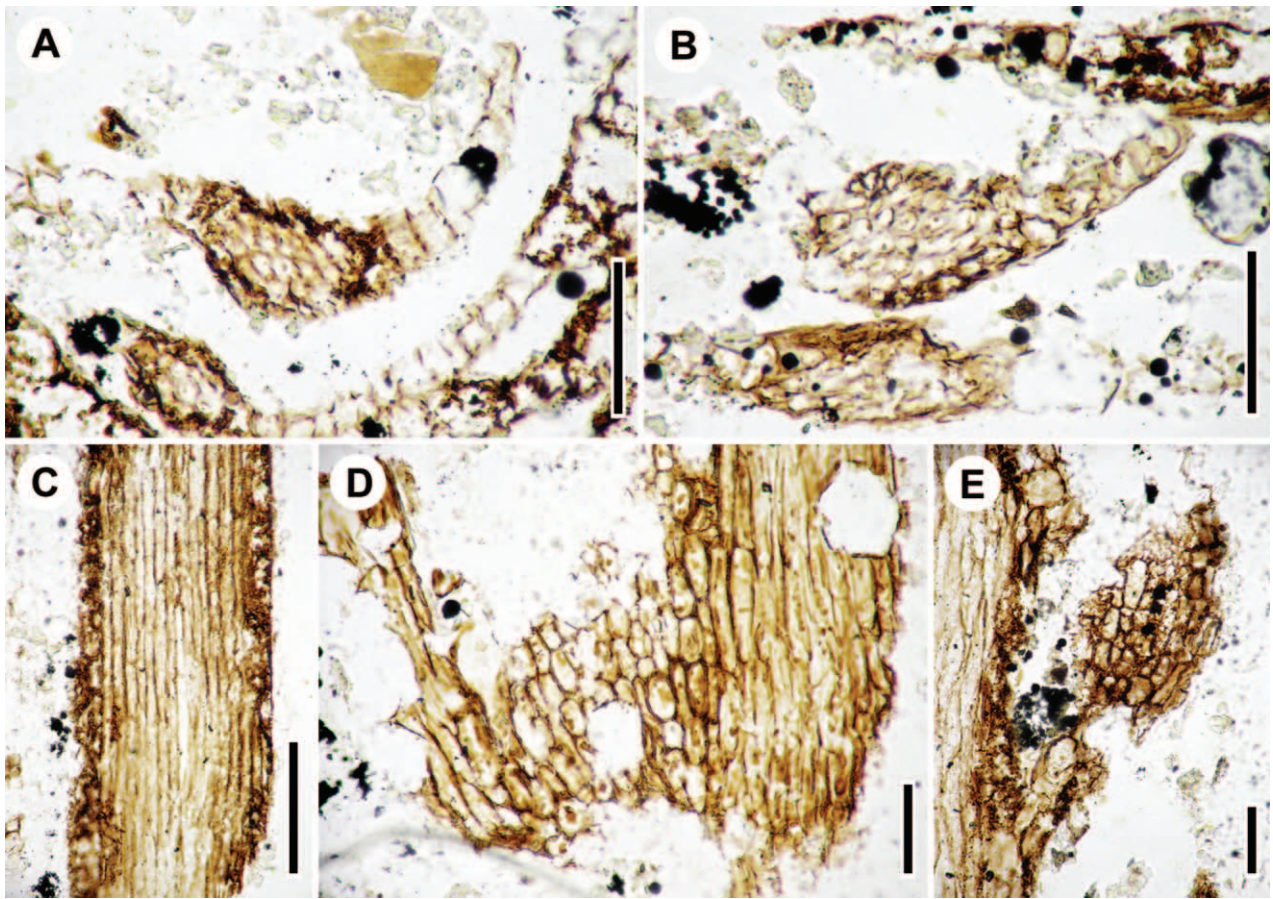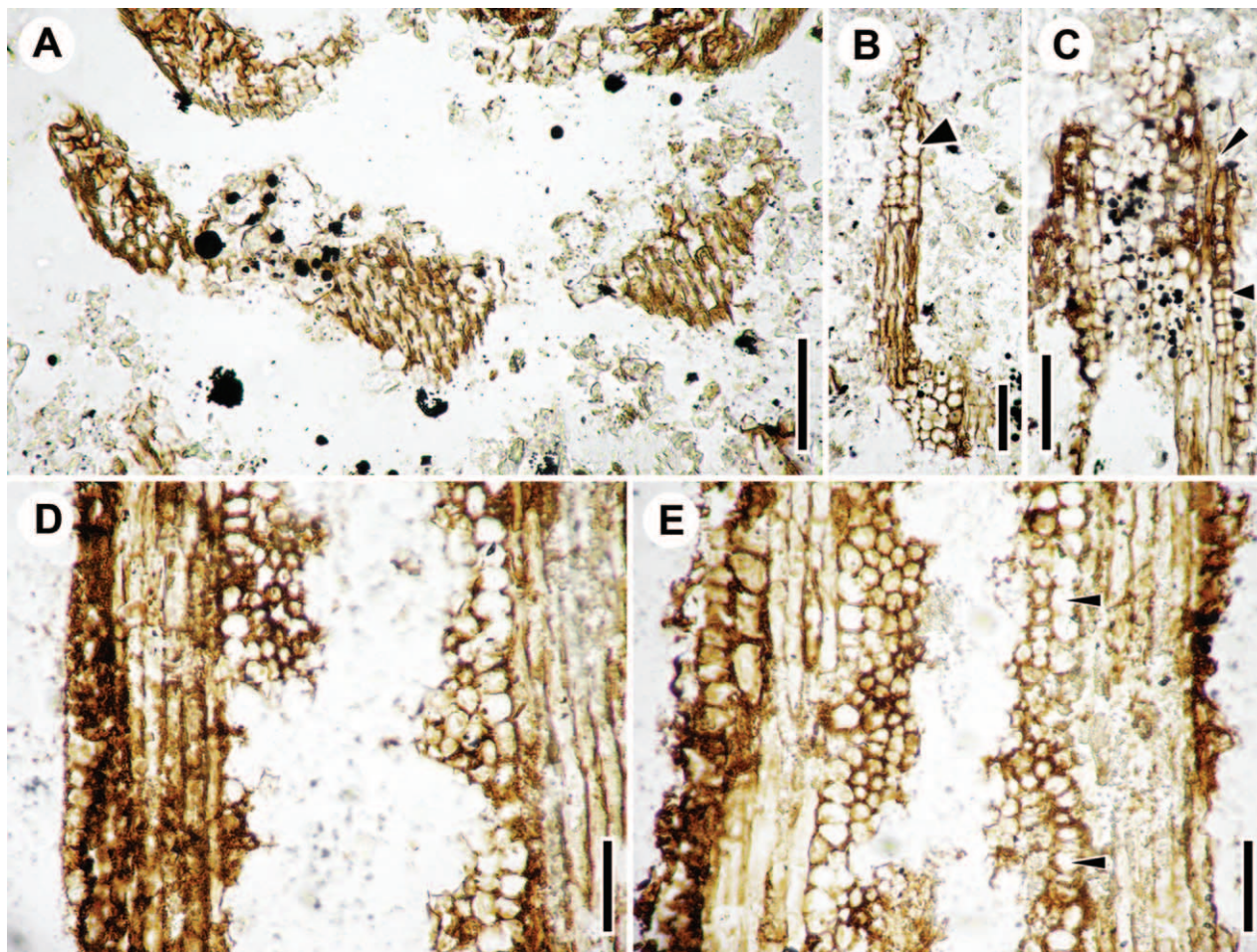
Fig. 8 Leaf anatomy of *Krassiloviella limbelloides* gen. et sp. nov. *A*, Leaf transverse section below the midleaf showing a slightly incurved leaf margin; note the darkened epidermis. P13131 D bot #22c. *B*, Transverse section of a plane leaf margin and lateral costa near midleaf; note the ab- and adaxial costal epidermis. P13131 D bot #22c. *C*, Longitudinal section through the central costa. P17596 C bot #66. *D*, Leaf base in paradermal section showing the central costa (*right*), the laminal cell morphology, and the lateral costa (*left*). P25 B bot #34b. *E*, Paradermal section of the incompletely preserved leaf base (stem at left) showing cells near the alar region just above the point of leaf attachment. P17596 D #30f. Scale bars: *A* = 100 μm; *B–E* = 50 μm.

permineralized shoots, with detailed preservation of numerous characters (e.g., branching architecture, leaf and stem anatomy, reproductive structures; Shelton et al. 2015). Comparisons between *K. limbelloides* and the other tricostate mosses (table 1) indicate that despite the shared tricostate condition, *K. limbelloides* is significantly different, thus warranting erection of a new genus.

Krassiloviella limbelloides shows similarities with some features that characterize individual *Tricostium* species, such as straight, lanceolate leaves with margins entire or toothed distally and leaves up to ca. 5 mm long and 1 mm wide with an acute apex and strong costae (table 1). However, several characters of *K. limbelloides* distinguish it from *Tricostium*: erect leaves with narrow divergence angles, a narrow leaf margin, wide costae merging in the leaf tip, and smooth laminal cells. Of the three *Tricostium* species, *K. limbelloides* is most similar to *Tricostium papillosum* Krassilov (Middle-Upper Jurassic, Russia; Krassilov 1973) but has longer leaves with a narrowly lanceolate shape (vs. ovate in *T. papillosum*), narrower leaf divergence angles, narrowly acute leaf apices, much wider costae that converge in the leaf apex, and smooth leaf cells (vs. pluripapillose in *T. papillosum*).

Comparisons with the anatomically preserved *T. plicata* reveal several similarities consistent with placement in the same family, Tricostaceae (see below), as well as numerous differences that justify segregation at the generic level. *Krassiloviella limbelloides* is most conspicuously different from *Tricosta* in having more delicate, erect, concave leaves up to 5 mm long with wider, thicker costae converging in the apex and laminal cells mostly isodiametric and forming longitudinal files (table 1). Furthermore, according to a survey of rhizoid positioning on pleurocarpous moss gametophytes (Ignatov and Hedenäs 2007), the presence of rhizoids adaxially on the costa in leaf axils is unusual; one rare exception is the genus *Scouleria*, in which some species exhibit rhizoids positioned both abaxially and adaxially on leaves and which also exhibits marginal

Fig. 9   Leaf anatomy of *Krassiloviella limbelloides* gen. et sp. nov. *A*, Composite image of leaf transverse section above midleaf showing three homogeneous costae and an incompletely preserved lamina. P13131 D bot #10c. *B*, Paradermal section near the leaf apex showing the laminal cells (*bottom*) and the isodiametric cells of the epidermis (arrowhead). P13131 D bot #19c. *C*, Paradermal section of the leaf apex showing few linear costal cells (thin arrowhead), laminal cells (*center*), and epidermal cells (thick arrowhead). P13131 D bot #23c. *D*, Leaf paradermal section near the midleaf showing the central costa (*right*), the median costa (*left*), and small isodiametric laminal cells; note the larger juxtacostal cells. P17596 C bot #66. *E*, Leaf paradermal section above the midleaf showing the central costa (*right*), the median costa (*left*), and small isodiametric laminal cells; larger juxtacostal cells are shown by the arrowheads. P17596 C bot #66. Scale bars = 50 μm.

multistratose thickenings of the leaf lamina, similar to the tricostate condition of *Krassiloviella* (Ignatova et al. 2015).

Pleurocarpy and Family-Level Placement

Taken alone, the pinnate branching, homocostate, and pluricostate leaves of *K. limbelloides* provide a strong case for pleurocarpy (Shelton et al. 2015), i.e., the production of gametangia on short, bud-like lateral branches (e.g., La Farge-England 1996; Newton 2007). Furthermore, several additional co-occurring features suggest pleurocarpous affinities for this species: main stems monopodial, the presence of second-order branching, stems without a conducting strand, and thin laminal cell walls. The combination of these features has been indicated as a proxy for pleurocarpy in the absence of sporophytes and based on an extensive survey of the bryological literature

(Shelton et al. 2015). Additional evidence in support of pleurocarpy in *Krassiloviella* comes from the specialized bud-like lateral branch preserved on one of the shoots. This incompletely preserved branch is probably a perichaetial branch bearing the remnants of archegonia. If that is true, the lateral position of the branch (fig. 10*A*) indicates pleurocarpy, as the production of archegonia on short, bud-like lateral branches is the defining feature of pleurocarpous mosses.

The hypnanaean family Tricostaceae was erected to accommodate much-branched, pleurocarpous, tricostate mosses (Shelton et al. 2015). Other than pleurocarpy, *K. limbelloides* features other characters diagnostic of Tricostaceae: regularly to irregularly pinnately branched stems, central conducting strand absent, thin-walled cortical cells, absence of hyalodermis or thick-walled outer cortex, paraphyllia absent, helically arranged leaves with three costae, and laminal cells never linear. One no-
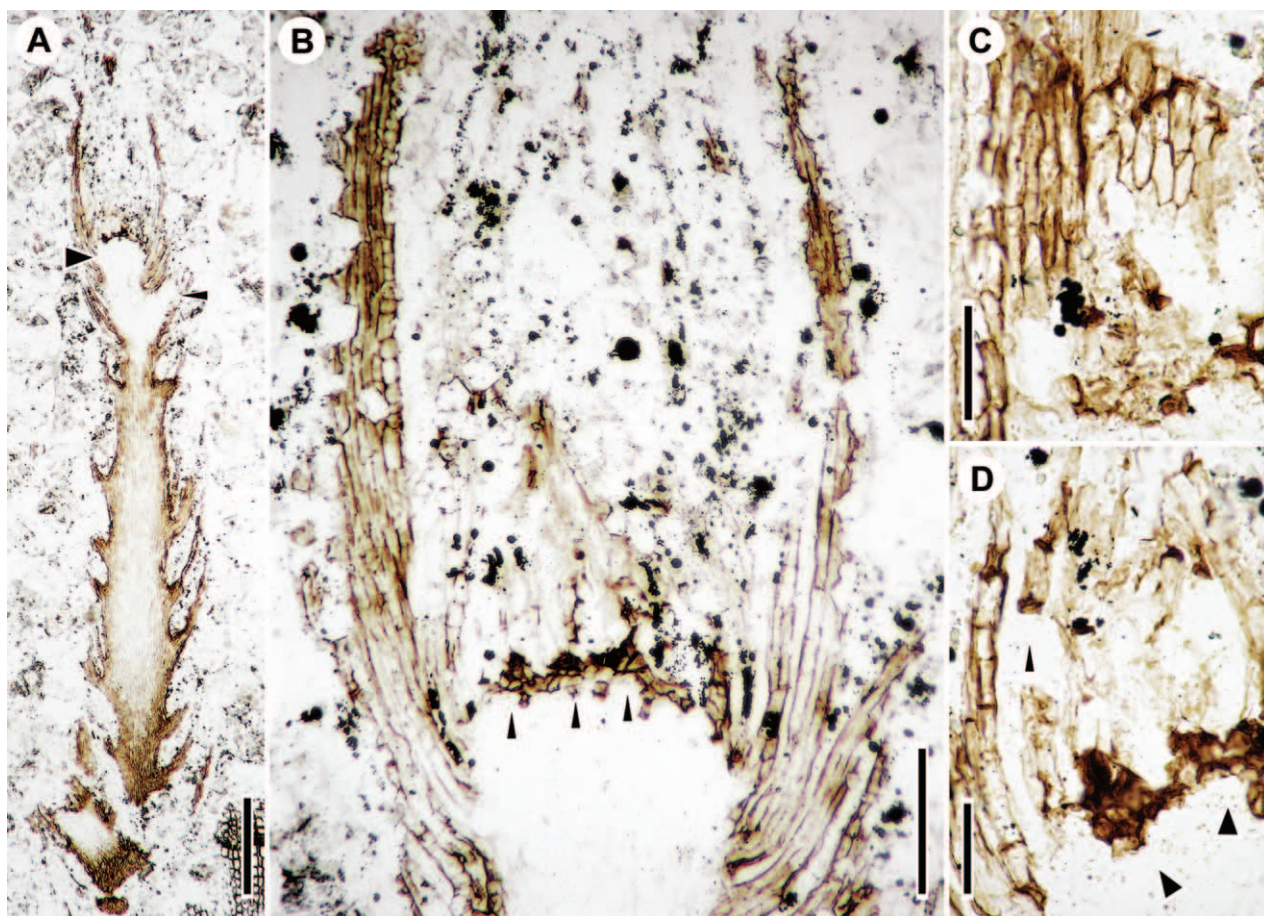
Fig. 10 Putative perichaetium of *Krassiloviella limbelloides* gen. et sp. nov. *A*, Longitudinal section of a shoot bearing a probable gametangial branch (thick arrowhead), subtended by a short branch (thin arrowhead); the tip of the main stem is not shown. Scale bar = 500 μm. P25 B bot #11b. *B*, Longitudinal section of the gametangial branch showing three bases of probable gametangia (arrowheads). Scale bar = 150 μm. P25 B bot #10b. *C*, Leaf cells in paradermal section from the probable gametangial branch. P25 B bot #6b. *D*, Probable uniseriate paraphysis (thin arrowhead) and gametangial bases (thick arrowheads). P25 B bot #11b. Scale bars: *C, D* = 50 μm.

table difference is that, whereas *K. limelloides* has inconspicuously differentiated alar regions, other species of the Tricostaceae have conspicuous alar regions. However, this difference is far outweighed by the similarities that support inclusion of *K. limelloides* in the Tricostaceae. Consequently, we have emended the familial diagnosis to include mosses with inconspicuous to well-defined alar regions.

Moss-Animal Interactions

One *Krassiloviella* specimen shows evidence of herbivory, likely by a microinvertebrate, in the form of a concave truncation of a shoot apex in which the outermost layers of remaining cells are darkened (fig. 4*A*, 4*D*). The continuity of the truncation across both stem and associated leaves strongly suggests that all these were removed in a single event by an herbivore (and not by fungal decomposition). For example, a stromatic structure or fungal fruiting body developed on the shoot tip would almost certainly leave behind remnants of hyphae in and on host tissues, and no such hyphae were found. The shoot tip was probably not removed by tapho-

nomic processes, because there are no characteristic signs of taphonomic breakage (e.g., crystal-shaped vacancies) at the tip. If the darkening of cells around the truncated area represents wound response by the plant, this would indicate that the interactions predated taphonomic processes. This is probably one of very few moss-animal interactions documented in the fossil record, especially for the pre-Cenozoic.

Outstanding Questions

The absence of extant mosses morphologically or anatomically equivalent to the extinct tricostate mosses, a relatively extensive group with at least eight distinct types known worldwide (Tomescu 2015; G. Shelton and A. Tomescu, personal observation), emphasizes the uniqueness of this group and raises questions about moss evolution. While such questions remain unanswered for now, they provide ideas for discussion and suggest directions for future studies in bryophyte development and morphology.

Why is the tricostate condition absent in extant mosses? Any attempt to answer this question should also explore what
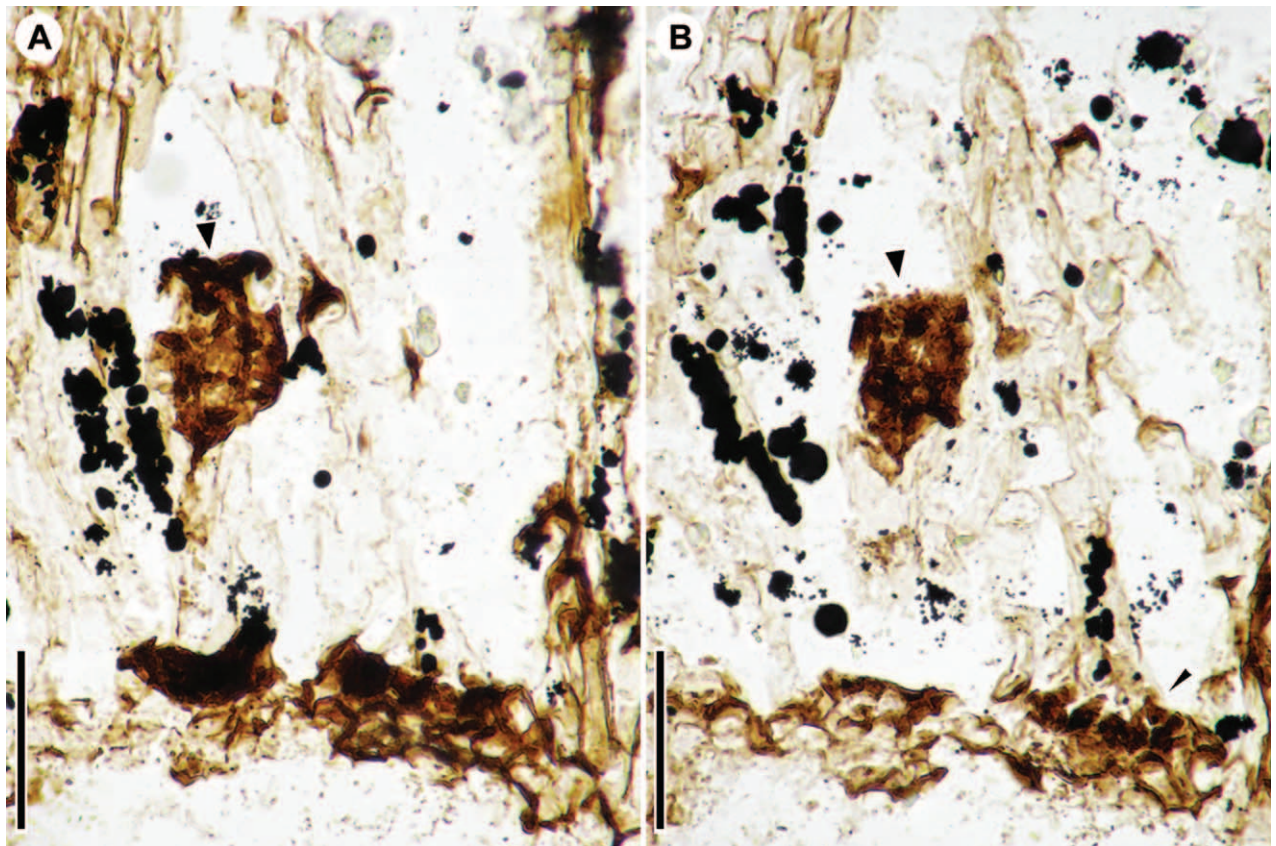
Fig. 11   Probable archegonial branch tip of *Krassiloviella limbelloides* gen. et sp. nov. *A*, Longitudinal section at the periphery of a specialized branch tip showing two dark bases (*bottom*); above the base at left is a dark several-celled structure (?embryo; arrowhead); the delicate pale tissue (*center*) probably represents remnants of several archegonia. P25 B bot #7b. *B*, Serial section adjacent to *A* showing two dark bases (*bottom*); the base at right is directly attached (thin arrowhead) to a column of pale tissue (archegonium) with a putative several-celled embryo (thick arrowhead). P25 B bot #8b. Scale bars = 50 μm.

kinds of functions, if any, this condition could have served. Three putative functions for strong costae developed along the entire leaf come to mind: (1) water conduction for faster diffusion throughout the leaf; (2) providing structural integrity, i.e., maintaining leaf shape during desiccation episodes and thus preventing irreparable damage due to excessive leaf deformation (shrinkage); and (3) enhancing mechanical resistance against abrasion in mosses that live in running water. Given the diminutive size of moss leaves, their water relations would probably not benefit significantly from specialized structures enhancing leaf conduction. Consequently, structural-mechanical functions would have more traction in explaining the presence of multiple costae, in an adaptive perspective. Indeed, Zastrow (1934) showed experimentally that when grown in an aquatic medium, costate mosses tend to develop ecostate leaves. This could be explained by the lack of both of the pressures that would favor development of a costa in drier conditions—i.e., no need for improved leaf conduction and absence of desiccation. However, not all ecostate mosses are aquatic, and some costate mosses are aquatic (e.g., Ochyra and Vanderpoorten 1999). Furthermore, species of several pleurocarpous genera, such as *Drepanocladus perplicatus* (Dusén) G. Roth,

Palustriella falcate (Brid.) Hedenäs, and *Vittia pachyloma* (Mont.) Ochyra, exhibit thickenings in the leaf lamina or along the leaf margin, especially when found in running water. Such thickenings may develop to protect against abrasion in such high-energy environments. Therefore, certain types of aquatic habitats may promote, rather than repress, development of leaf thickenings.

Do trends in the presence of costae provide any insight into their evolutionary history? In the broadest sense, extant mosses illustrate a trend from ecostate leaves in the most basal lineages (Takakiopsida, Sphagnopsida, Andreaeopsida) to costate leaves in more derived lineages (Oedipodiopsida, Polytrichopsida, Bryopsida). However, some lineages within these groups illustrate independent instances of further reduction or elaboration of the costa (Goffinet et al. 2009; Olsson et al. 2009). Furthermore, the oldest mosses known to date in the fossil record have costate leaves (Hübers and Kerp 2012). Clearly, a denser stratigraphic and taxonomic sampling of the moss fossil record is needed to test for the presence of evolutionary trends in moss leaf morphology.

Do all costae share the same developmental pathway, and are there anatomical signatures for the mode of development

Table 1

Krassiloviella limbelloides gen. et sp. nov. Compared to Tricosta plicata and Species of Tricostium

	Krassiloviella limbelloides	Tricosta plicata	Tricostium longifolium	Tricostium papillosum	Tricostium triassicum
Stem length (min.)	20 mm	22 mm	10 mm	3.9 mm	?
Branch length (min.)	.3–1 mm	.5 mm	5.5–7.5 mm	1.3 mm	?
Distance between branches (min.)	.8–4.0 mm	.5 mm	5.0 mm	?	?
Stem width	370–430 μm	Ca. 200 μm	Ca. 300 μm	?	?
Branching angle	25°–45°	(41°)–55°–(75°)	Ca. 25°–35° (60°)	Ca. 43°	?
Density of foliation	4.5–6 leaves/mm	Dense, (11)–18–(23) leaves/mm	Sparse; ca. 1.6 leaves/mm	Dense, ca. 3–5 leaves/mm	?
Leaf divergence	±Erect (5°–20°)	Erect-spreading (38°)-45°-(55°)	Patent-recurved (15°–45° at base with distal half of leaf recurred)	Patent (ca. 25°–40°)	?
Leaf orientation	Straight	Straight	Recurved	Straight	
Leaf shape	Narrowly lanceolate	Ovate	Lanceolate	Ovate (to narrowly ovate)	Narrowly lanceolate (?or oblong)
Leaf relief	Concave	Plicate	Some keeled	Flat (?slightly undulate)	Flat (?to concave)
Leaf margin	Probably entire from base to near apex; minute dentition in apex	Probably entire	?	Distally serrate (or entire)	Entire in at least middle and near base
Leaf length	Ca. 4 mm (up to 5 mm)	Ca. 2 mm	4–6 mm	Ca. 1.2 mm (up to 1.8 mm)	4–5 mm
Leaf width	Up to .9 mm	.8–1.0 mm	Up to 1.5 mm	Ca. .5 mm (up to 1 mm in some fragments)	.9 mm
Leaf apex	Acute (tip apiculate)	Acute (?to acuminate)	Acute	Obtuse to acute	Acute?
Leaf base	Clasping	Clasping (minutely auriculate)	Truncate?	Clasping (?or auriculate)	Truncate?
Median costa length (ratio of leaf length)	At least .95, percurrent	At least .95 (failing to percurrent)	At least .9	.9–.95 (failing to percurrent)	At least .8
Median costa width	70–125 μm	Ca. 54 μm	60–80 μm	Ca. 50 μm	80 μm
Lateral costa length	At least .95, percurrent; merging with central costa in leaf apex	At least .9	At least .9	.7–.9	>At least .8
Lateral costa width	50–80 μm	Ca. 35 μm	Ca. 25 μm	Ca. 20–30 μm	30–40 μm
Alar region	Inconspicuous; cells oval, irregular, or isodiametric, 12–24 (up to 40) μm long, 12 (up to 16) μm wide, 2.5:1	Conspicuous; cells inflated, globose to cylindric, diameters 15–32 μm (up to 54 μm long)	?	?	?
Lamina cell arrangement	Longitudinal files	Oblique files near midleaf; longitudinal files in distal half	?Oblique files	Longitudinal files	Longitudinal files
Lamina cell shapes	Oval, isodiametric, or quadrate	Rhombic, repand, oval to isodiametric	Isodiametric (?rounded or polygonal)	Polygonal, isodiametric	Quadrate to short rectangular
Lamina cell shape ratio and size	Up to 4:1 basally (40 μm); 1.33:1 and 8–12 μm lengths (up to 18 μm) above the base	Up to 5:1 (40 μm) basally; 2–3:1 at midleaf (ca. 25 μm and up to 35 μm); isodiametric and up to 23 μm distally	13–17 μm	15–18 μm	Ca. 13–16 μm wide
Lamina cell wall thickenings	Absent	Absent	?	?Thickened corners	?
Lamina cell surface texture	Smooth	Smooth	?	Pluripapillate (8–10 papillae per cell)	?

Note.   Data from Krassilov (1973); Ignatov and Shcherbakov (2011a, 2011b); Shelton et al. (2015).

of the costa, which could be used to understand development of these structures in fossil mosses? Some costae have been shown to form early in leaf development, by periclinal divisions in specific regions of the unistratose leaf primordia (Frey 1970). In contrast, multistratose streaks in the leaf lamina (or leaf margin) are thought to be formed later in development (Goffinet et al. 2009). Developmental information of this type is not available for *Krassiloviella*, and even if it was, the very few studies of leaf development in extant mosses do not allow for conclusive inferences on developmental differences diagnostic of costae versus multistratose streaks.

Finally, within the pleurocarpous mosses, how well do gametophytic characters reflect phylogeny? More broadly, this question relates to the fundamental conundrum raised in the taxonomic placement of many fossil mosses by the severe disparity between characters used by "neo"-bryologists and those available to paleobotanists. In the particular case of *Krassiloviella*, the absence of sporophytic characters, widely used in family-level taxonomy of extant mosses, precludes traditional comparisons and unequivocal placement within the pleurocarpous mosses. The alternative to this is a comparison based on gametophytic characters, whose inclusion in phylogenetic studies is not uncommon (e.g., Hedenäs 1994; Newton and De Luna 1999). It is encouraging that over the past two decades a steady output of empirical studies have addressed the relationships between morphological characters (of both gametophytes and sporophytes), on the one hand, and systematic relationships, growth environment, and growth habit, on the other hand, in ca. 10% of known pleurocarp species (Hedenäs 1999, 2001*a*, 2001*b*, 2002, 2012; Hedenäs and Bisang 2015). Continued work in this direction will significantly strengthen the morphoanatomical framework of moss taxonomy and improve the precision of taxonomic placement of fossil mosses, many of which are known only by their gametophyte phase.

Conclusions

Krassiloviella limbelloides is the second bryophyte described from the Early Cretaceous Apple Bay flora of Vancouver Island, as well as the second genus of the hypnanaean moss family Tricostaceae. *Krassiloviella* corroborates the original diagnosis of the family (Shelton et al. 2015), while also broadening the range of variation of alar cells, which led to emendation of the familial diagnosis. Discovery of a second representative of the Tricostaceae reinforces the conclusions reached based on the original description of the family as the oldest unequivocal evidence for the pleurocarpous superorder Hypnanae that provides a hard minimum age for the group.

Considered against the background of the sparse pre-Cenozoic moss fossil record, these discoveries reinforce ideas that the extant flora does not hold the complete answer to the overall patterns of bryophyte diversity over space and time. The fossil record reveals moss diversity unaccounted for in extant floras, reaffirming the contribution of paleontology to efforts aimed at documenting the history of biodiversity. Well-characterized fossil species are also key to addressing patterns of deep phylogeny, by broadening the range of taxon sampling by adding lineages with novel combinations of characters that could not have been foreseen from surveys based on extant plants alone.

The quality of fossil preservation at the Early Cretaceous Apple Bay locality allows for detailed reconstructions and thorough discussions of the evolution of anatomical features otherwise lost to harsher taphonomic processes. The preservation of minute and extremely delicate structures such as bryophyte antheridia (Shelton et al. 2015) and photobiont-mycobiont interfaces in lichen thalli (Matsunaga et al. 2013) is a testament to this, as is the evidence of herbivory and perichaetia in *K. limbelloides*. The accessibility of this level of detail is promising for ongoing studies aimed at resolving the taxonomy and characterizing the life history of Early Cretaceous bryophytes and cryptogams from Apple Bay.

Acknowledgments

Literature Cited

Atkinson BA, GW Rothwell, RA Stockey 2014*a* *Hubbardiastrobus cunninghamioides* gen. et sp. nov., evidence for a Lower Cretaceous diversification of cunninghamioid Cupressaceae. Int J Plant Sci 175:256–269.

———— 2014*b* *Hughmillerites vancouverensis* sp. nov. and the Cretaceous diversification of Cupressaceae. Am J Bot 101:2136–2147.

Bronson AW, AA Klymiuk, RA Stockey, AMF Tomescu 2013 A perithecial sordariomycete (Ascomycota, Diaporthales) from the Lower Cretaceous of Vancouver Island, British Columbia, Canada. Int J Plant Sci 174:278–292.

Carter BE, S Nosratinia, JR Shevock 2014 A revisitation of species circumscriptions and evolutionary relationships in *Scouleria* (Scouleriaceae). Syst Bot 39:4–9.

Churchill SP 1985 The systematics and biogeography of *Scouleria* Hook. (Musci: Scouleriaceae). Lindbergia 11:59–71.

Frey W 1970 Blattenwicklung bei Laubmoosen. Nova Hedwigia 20: 463–556.

Goffinet B, WR Buck, AJ Shaw 2009 Morphology, anatomy, and classification of the Bryophyta. Pp. 55–138 *in* B Goffinet, AJ Shaw, eds. Bryophyte biology. 2nd ed. Cambridge University Press, Cambridge.

Gradstein SR, SP Churchill, N Salazar-Allen 2001 Guide to the bryophytes of tropical America. New York Botanical Garden Press, New York.

Greuter W, J McNeill, FR Barrie, H-M Burdet, V Demoulin, TS Filgueiras, DH Nicolson, et al 2000 International code of botanical nomenclature (Saint Louis code). International Association for Plant Taxonomy. Koeltz Scientific, Königstein, Germany.

Hastings RI, H Deguchi 1997 Taxonomy of *Coscinodon arctolimnius* (Bryopsdia, Grimmiaceae) including a new subspecies from Asia. Bryologist 100:50–55.

Hedenäs L 1994 The basal pleurocarpous diplolepidous mosses—a cladistic approach. Bryologist 97:225–243.

——— 1999 How important is phylogenetic history in explaining character states in pleurocarpous mosses? Can J Bot 77:1723–1743.

——— 2001a Environmental factors potentially affecting character states in pleurocarpous mosses. Bryologist 104:72–91.

——— 2001b The importance of phylogeny and habitat factors in explaining gametophytic character states in European Amblystegiaceae. J Bryol 23:205–219.

——— 2002 Important complexes of intercorrelated character states in pleurocarpous mosses. Lindbergia 27:104–121.

——— 2012 Morphological and anatomical features associated with epiphytism among the pleurocarpous mosses—one basis for further research on adaptations and their evolution. J Bryol 34:79–100.

Hedenäs L, I Bisang 2015 Are morphology and environment correlated with male dwarfism in pleurocarpous mosses? Arctoa 24:362–374.

Hedenäs L, J Heinrichs, AR Schmidt 2014 Bryophytes of the Burmese amber forest: amending and expanding the circumscription of the Cretaceous moss genus *Vetiplanaxis*. Rev Paleobot Palynol 209:1–10.

Hernandez-Castillo GR, RA Stockey, GW Rothwell 2006 *Anemia quatsinoensis* sp. nov. (Schizaeaceae), a permineralized fern from the Lower Cretaceous of Vancouver Island. Int J Plant Sci 167:665–674.

Hübers M, H Kerp 2012 Oldest known mosses discovered in Mississippian (late Visean) strata of Germany. Geology 40:755–758.

Ignatov MS 1990 Upper Permian mosses from the Russian Platform. Palaeontographica B 217:147–189.

Ignatov MS, L Hedenäs 2007 Homologies of stem structures in pleurocarpous mosses, especially of pseudoparaphyllia and similar structures. Pp. 269–286 *in* AE Newton, RS Tangney, eds. Pleurocarpous mosses: systematics and evolution. CRC, Boca Raton, FL.

Ignatov MS, EV Karasev, SM Sinitsa 2011 Upper Jurassic mosses from Baigul (Transbaikalia, south Siberia). Arctoa 20:43–64.

Ignatov MS, DE Shcherbakov 2007 Did pleurocarpous mosses originate before the Cretaceous? Pp. 321–336 *in* AE Newton, RS Tangney, eds. Pleurocarpous mosses: systematics and evolution. CRC, Boca Raton, FL.

——— 2011a Lower Cretaceous mosses from Khasurty (Transbaikalia). Arctoa 20:19–42.

——— 2011b Lower Triassic mosses from Yaman Us (Mongolia). Arctoa 20:65–80.

Ignatova EA, LE Kurbatova, OI Kuznetsova, OV Ivanov, JR Shevock, BE Carter, MS Ignatov 2015 The genus *Scouleria* (Bryophyta) in Russia revisited. Arctoa 24:47–66.

Joy KW, AJ Willis, WS Lacey 1956 A rapid cellulose peel technique in palaeobotany. Ann Bot 20:635–637.

Klymiuk AA, RA Stockey 2012 A Lower Cretaceous (Valanginian) seed cone provides the earliest fossil record for *Picea* (Pinaceae). Am J Bot 99:1069–1082.

Klymiuk AA, RA Stockey, GW Rothwell 2015 Plant-arthropod interactions in *Acanthostrobus edenensis* (Cupressaceae), a new conifer from the Upper Cretaceous of Vancouver Island, British Columbia. Int J Plant Sci 176:378–392.

Konopka AS, PS Herendeen, PR Crane 1998 Sporophytes and gametophytes of Dicranaceae from the Santonian (Late Cretaceous) of Georgia, U.S.A. Am J Bot 85:714–723.

Konopka AS, PS Herendeen, GL Smith Merrill, PR Crane 1997 Sporophytes and gametophytes of Polytrichaceae from the Campanian (Late Cretaceous) of Georgia, U.S.A. Int J Plant Sci 158:489–499.

Krassilov VA 1973 Mesozoic bryophytes from the Bureja Basin, Far East of the USSR. Palaeontographica B 143:95–105.

La Farge-England C 1996 Growth form, branching pattern and perichaetial position in mosses: cladocarpy and pleurocarpy redefined. Bryologist 99:170–186.

Lawton E 1971 Moss flora of the Pacific Northwest. Hattori Botanical Laboratory, Nichinan, Japan.

Little SA, RA Stockey, GW Rothwell 2006a *Solenostelopteris skogiae* sp. nov. from the Lower Cretaceous of Vancouver Island. J Plant Res 119:525–532.

——— 2006b *Strameniopteris aureopilosus* gen. et sp. nov.: reevaluating the role of vegetative anatomy in the resolution of leptosporangiate fern phylogeny. Int J Plant Sci 167:683–694.

Matsunaga KS, RA Stockey, AMF Tomescu 2013 *Honeggeriella complexa* gen. et sp. nov., a heteromerous lichen from the Lower Cretaceous of Vancouver Island (British Columbia, Canada). Am J Bot 100:450–459.

Matteri CM 1979 Notas briológicas (Musci). IV, V. Bryologist 82:99–102.

Newton AE 2007 Branching architecture in pleurocarpous mosses. Pp. 287–307 *in* AE Newton, RS Tangney, eds. Pleurocarpous mosses: systematics and evolution. CRC, Boca Raton, FL.

Newton AE, E De Luna 1999 A survey of the morphological characters for phylogenetic study of the transition to pleurocarpy. Bryologist 102:651–682.

Ochyra R, A Vanderpoorten 1999 *Platyhypnidium mutatum*: a mysterious new moss from Germany. J Bryol 21:183–189.

Olsson S, V Buchbender, J Enroth, S Huttunen, L Hedenäs, D Quandt 2009 Evolution of the Neckeraceae (Bryophyta): resolving the backbone phylogeny. Syst Biodivers 7:419–432.

Oostendorp C 1987 The bryophytes of the Palaeozoic and the Mesozoic. Bryophyt Bibl 34:1–112.

Ray MM, GW Rothwell, RA Stockey 2014 Anatomically preserved Early Cretaceous bennettitalean leaves: *Nilssoniopteris corrugata* n. sp. from Vancouver Island, Canada. J Paleontol 88:1085–1093.

Rothwell GW, WL Crepet, RA Stockey 2009 Is the anthophyte hypothesis alive and well? new evidence from the reproductive structures of Bennettitales. Am J Bot 96:296–322.

Rothwell GW, RA Stockey 2006 Combining characters of Pteridaceae and tree ferns: *Pteridorus radiata* gen. et sp. nov., a permineralized Lower Cretaceous filicalean with radial sori. Int J Plant Sci 167:695–701.

——— 2010 Independent evolution of seed enclosure in Bennettitales: evidence from the anatomically preserved cone *Foxeoidea connatum* gen. et sp. nov. Pp. 51–66 *in* CT Gee, ed. Plants in Mesozoic time: innovations, phylogeny, ecosystems (Ted Delevoryas festschrift). Indiana University Press, Bloomington.

——— 2013 Evolution and phylogeny of gnetophytes: evidence from the anatomically preserved seed cone *Protoephedrites eamesii* gen. et sp. nov. and the seeds of several bennettitalean species. Int J Plant Sci 174:511–529.

Rothwell GW, RA Stockey, MA Millay 2014 Evolution of modern Marattiales; superficially *Christensenia*-like synangia in the Early Cretaceous. Paper presented at the Botanical Society of America 2014 conference, Boise, ID. http://2014.botanyconference.org/engine/search/index.php?func=detail&aid=283.

Rubinstein CV, P Gerrienne, S de la Puente, RA Astini, P Steemans 2010 Early Middle Ordovician evidence for land plants in Argentina (eastern Gondwana). New Phytol 188:365–369.

Shelton GWK, RA Stockey, GW Rothwell, AMF Tomescu 2015 Exploring the fossil history of pleurocarpous mosses: Tricostaceae fam. nov. from the Cretaceous of Vancouver Island, Canada. Am J Bot 102:1883–1900.

Smith SY, RS Currah, RA Stockey 2004 Cretaceous and Eocene poroid hymenophores from Vancouver Island, British Columbia. Mycologia 96:180–186.

Smith SY, GW Rothwell, RA Stockey 2003 *Cyathea cranhamii* sp. nov. (Cyatheaceae), anatomically preserved tree fern sori from

the Lower Cretaceous of Vancouver Island, British Columbia. Am J Bot 90:755–760.

Smoot EL, TN Taylor 1986 Structurally preserved fossil plants from Antarctica. II. A Permian moss from the Transantarctic Mountains. Am J Bot 73:1683–1691.

Stanich NA, GW Rothwell, RA Stockey 2009 Phylogenetic radiation of *Equisetum* (Equisetales) as inferred by Lower Cretaceous species from British Columbia, Canada. Am J Bot 96:1289–1299.

Stockey RA 2004 Anatomically preserved pteridophytes: unexpected diversity for the Early Cretaceous. Pages 25–26 *in* Ferns for the 21st Century: an International Symposium on Pteridophytes. Royal Botanic Garden, Edinburgh, United Kingdom.

Stockey RA, GW Rothwell 2009 Distinguishing angiophytes from the earliest angiosperms: a Lower Cretaceous (Valanginian-Hauterivian) fruit-like reproductive structure. Am J Bot 96:323–335.

Stockey RA, GW Rothwell, SA Little 2006 Relationships among fossil and living Dipteridaceae: anatomically preserved *Hausmannia* from the Lower Cretaceous of Vancouver Island. Int J Plant Sci 167:649–663.

Stockey RA, NJB Wiebe 2008 Lower Cretaceous conifers from Apple Bay, Vancouver Island: *Picea*-like leaves, *Midoriphyllum piceoides* gen. et sp. nov. (Pinaceae). Botany 86:649–657.

Strother PK, S Al-Hajri, A Traverse 1996 New evidence for land plants from the lower Middle Ordovician of Saudi Arabia. Geology 24:55–58.

Taylor TN, EL Taylor, M Krings 2009 Paleobotany: the biology and evolution of fossil plants. 2nd ed. Academic Press, Burlington, MA.

Tomescu AMF 2015 Looking behind the tracheophyte curtain: a renewed focus on the bryophyte fossil record. Paper presented at the Botanical Society of America 2015 conference, Edmonton, Alberta, Canada. http://2015.botanyconference.org/engine/search/index.php?func=detail&aid=379.

Tomescu AMF, CM Steenbock, M Friedman, RA Stockey 2012 The Early Cretaceous Apple Bay flora of Vancouver Island: a hotspot of fossil bryophyte diversity. Paper presented at the Botanical Society of America 2012 conference, Columbus, OH. http://2012.botanyconference.org/engine/search/index.php?func=detail&aid=962.

Vavrdova M 1990 Coenobial acritarchs and other palynomorphs from the Arenig/Llanvirn boundary, Prague Basin. Vestnik Ustred Ustava Geol 65:237–242.

Vavrek MJ, RA Stockey, GW Rothwell 2006 *Osmunda vancouverensis* sp. nov. (Osmundaceae), permineralized fertile frond segments from the Lower Cretaceous of British Columbia, Canada. Int J Plant Sci 167:631–637.

Wellman CH, PL Osterloff, U Mohiuddin 2003 Fragments of the earliest land plants. Nature 425:282–285.

Zastrow E 1934 Experimentelle Studien über die Anpassung von Wasser—und Sumpfmoosen. Pflanzenforschung 17:1–70.