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Abstract:	<p>Premise of the study: Mosses, very diverse in modern ecosystems, are currently underrepresented in the fossil record. For the pre-Cenozoic, fossil mosses are known almost exclusively from compression fossils, while anatomical preservation, which is much more taxonomically informative, is rare. The Lower Cretaceous of Vancouver Island (British Columbia, Canada) hosts a diverse anatomically preserved flora at Apple Bay. While the vascular plant component of the Apple Bay flora has received much attention, the numerous bryophytes identified at the locality have yet to be characterized.</p> <p>Methods: Fossil moss gametophytes in more than 20 carbonate concretions collected from the Apple Bay locality on Vancouver Island were studied in serial sections prepared using the cellulose acetate peel technique.</p> <p>Key results: We describe <i>Tricosta plicata</i> gen. et sp. nov., a pleurocarpous moss with much-branched gametophytes, tricostate plicate leaves, rhizoid-bearing bases, and delicate gametangia (antheridia and archegonia) borne on specialized branches. A new family of hypnanaean mosses, Tricostaceae fam. nov., is recognized based on the novel combination of characters of <i>T. plicata</i>.</p> <p>Conclusions: <i>Tricosta plicata</i> reveals pleurocarpous moss diversity unaccounted for in extant floras. This new moss adds the first bryophyte component to an already diverse assemblage of vascular plants described from the Early Cretaceous at Apple Bay and, as the oldest representative of the Hypnanae, provides a hard minimum age for the group (136 Ma).</p>

1 Shelton et al. – Cretaceous tricostate pleurocarpous mosses

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4 **Exploring the fossil history of pleurocarpous mosses: Tricostaceae fam. nov. from the**
5 **Cretaceous of Vancouver Island, Canada¹**

6

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22

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24 in the fossil record. For the pre-Cenozoic, fossil mosses are known almost exclusively from
25 compression fossils, while anatomical preservation, which is much more taxonomically
26 informative, is rare. The Lower Cretaceous of Vancouver Island (British Columbia, Canada)
27 hosts a diverse anatomically preserved flora at Apple Bay. While the vascular plant component
28 of the Apple Bay flora has received much attention, the numerous bryophytes identified at the
29 locality have yet to be characterized.

30 *Methods:* Fossil moss gametophytes in more than 20 carbonate concretions collected from the
31 Apple Bay locality on Vancouver Island were studied in serial sections prepared using the
32 cellulose acetate peel technique.

33 *Key results:* We describe *Tricosta plicata* gen. et sp. nov., a pleurocarpous moss with much-
34 branched gametophytes, tricostate plicate leaves, rhizoid-bearing bases, and delicate gametangia
35 (antheridia and archegonia) borne on specialized branches. A new family of hypnanaean
36 mosses, Tricostaceae fam. nov., is recognized based on the novel combination of characters of *T.*
37 *plicata*.

38 *Conclusions:* *Tricosta plicata* reveals pleurocarpous moss diversity unaccounted for in extant
39 floras. This new moss adds the first bryophyte component to an already diverse assemblage of
40 vascular plants described from the Early Cretaceous at Apple Bay and, as the oldest
41 representative of the Hypnanae, provides a hard minimum age for the group (136 Ma).

42

43 **Key words:** Bryophyta; Cretaceous; fossil; gametangia; Hypnanae; moss; pleurocarpous;
44 tricostate

45

46 Bryophytes pre-date the vascular plants and the fossil record of mosses can be traced
47 back in time for at least 330 million years, into the Early Carboniferous (Hübers and Kerp,
48 2012). However, the long history of mosses is not matched by a corresponding richness of the
49 fossil record of the group, especially for pre-Cenozoic times. Compared to an estimated 13,000
50 extant moss species (Goffinet et al., 2009) and to relatively numerous Cenozoic fossil mosses
51 (many of which represent modern families, genera, and species; e.g., Miller, 1984; Taylor et al.,
52 2009), the pre-Cenozoic moss fossil record, with only ca. 70 described species (e.g., Oostendorp,
53 1987; Ignatov, 1990; Taylor et al., 2009), represents a small fraction of known moss diversity.
54 Considered in light of the long evolutionary history of the group, the marked scarcity of pre-
55 Cenozoic mosses indicates that we are still missing most of the diversity representing the first
56 270 million years (to use a conservative estimate) of evolution in the group. Yet, only by
57 discovering and characterizing this hidden diversity will we be able to understand patterns of
58 moss diversity and evolution in deep time, with all their implications for understanding extant
59 moss diversity. Paleobotanical studies of fossil mosses are our only way to access this hidden
60 world of biological diversity that would remain unattainable otherwise.

61 Pre-Cenozoic fossil mosses are rarely placed into modern groups or such taxonomic
62 assignments are tentative. Nevertheless, some of these fossils resemble modern groups or well-
63 defined extinct lineages, demonstrating a potential to contribute to moss systematics. For
64 example, the oldest unequivocal moss fossils represent leaf fragments from the Lower
65 Carboniferous (Middle Mississippian, late Visean) of eastern Germany (Hübers and Kerp, 2012),
66 some of which resemble the extinct Protosphagnales Neuburg, perhaps representing forms
67 ancestral to both sphagnalean and non-sphagnalean mosses. In the Upper Jurassic of Russia,
68 *Baigulia* Ignatov, Karasev et Sinitza and *Bryokhutuliinia ingodensis* Ignatov show highly

69 branched gametophytes and lateral bud-like structures interpreted as gametangial shoots (Ignatov
70 et al., 2011). These fossil mosses, along with *Vetiplanaxis* N.E. Bell, are the only pre-Cenozoic
71 that have putative affinities with the pleurocarpous mosses – a large group of mosses in which
72 sporophytes are borne on reduced lateral shoots of gametophyte stems.

73 To date, Cretaceous moss diversity consists of less than ten genera (e.g., Ettingshausen
74 and Debey, 1859; Berry, 1928; Krassilov, 1973; 1982; Ignatov et al., 2011; Ignatov and
75 Shcherbakov, 2011a), few of which preserve enough detail to support ordinal or family-level
76 placement. Species of *Vetiplanaxis*, a late Albian genus known from Burmese amber, are most
77 comparable to the pleurocarpous Hypnodendrales (Hedenäs et al., 2014). Charcoalified
78 gametophytes and sporophytes of *Campylopodium allonense* Konopka, Herendeen et Crane
79 (1998) and *Eopolytrichum antiquum* Konopka, Herendeen, Merrill et Crane (1997) from the late
80 Santonian of Georgia (USA) are assigned unequivocally to the families Dicranaceae and
81 Polytrichaceae, respectively. Overall, we currently have a very incomplete image of what
82 Cretaceous mosses looked like or where they fit among bryophytes and, therefore, of what they
83 could teach us about moss diversity and evolution over time.

84 In terms of modes of preservation, most of the moss fossil record is represented by
85 carbonaceous compressions. Anatomically preserved pre-Cenozoic moss fossils are rare and,
86 prior to this study, have been limited to cuticular preservation of Mississippian moss leaves
87 (Hübers and Kerp, 2012); charcoalified Late Cretaceous gametophytes and sporophytes
88 (Konopka et al., 1997; 1998); permineralized Permian gametophytes of *Merceria augustica*
89 Smoot et Taylor (1986); and amber preservation of mid-Cretaceous gametophytes (Hedenäs et
90 al., 2014).

91 There is a growing realization that exquisitely preserved plant remains are present in

92 marine carbonate concretions from Jurassic, Cretaceous, Paleogene, and Neogene sediments
93 worldwide (e.g., Stockey and Rothwell, 2006), many of which contain remains of anatomically
94 preserved bryophytes (e.g., Steenbock et al., 2011; Tomescu et al., 2012). Here we describe an
95 anatomically preserved Early Cretaceous moss based on abundant permineralized specimens
96 from the Apple Bay locality (Vancouver Island, British Columbia, Canada). This moss is
97 described as a new genus and species characterized by highly branched gametophytes with
98 perigonia and perichaetia on short lateral, bud-like branches, and tricostate leaves, a trait not
99 recognized in extant mosses and documented only in a few Mesozoic fossils. It is one of the
100 most complete pre-Cenozoic fossil mosses to date and represents the earliest record for
101 pleurocarpy, as well as a new family within superorder Hypnanae. Along with other tricostate
102 mosses (fossil genus *Tricostium* Krassilov), this moss brings to light a once widespread aspect of
103 moss morphological diversity unknown in the extant bryoflora.

104 MATERIALS AND METHODS

105 Numerous moss gametophyte shoots are preserved by cellular permineralization in >23
106 carbonate concretions, as part of an allochthonous fossil assemblage deposited in nearshore
107 marine sediments (e.g., Stockey and Rothwell, 2009). The concretions were collected from
108 sandstone (greywacke) beds exposed on the northern shore of Apple Bay, Quatsino Sound, on
109 the west side of Vancouver Island, British Columbia, Canada (50°36'21" N, 127°39'25" W;
110 UTM 9U WG 951068) (e.g., Stockey and Rothwell, 2009). The layers containing the
111 concretions are regarded as Longarm Formation equivalents and have been dated by oxygen
112 isotope analyses to the Valanginian (Early Cretaceous, ca. 136 Ma) (Stockey et al., 2006; D.
113 Gröcke pers. comm., 2013).

114 This Early Cretaceous flora includes lycophytes, equisetophytes, at least 10 families of

115 ferns (Smith et al., 2003; Hernandez-Castillo et al., 2006; Little et al., 2006a, 2006b; Rothwell
116 and Stockey, 2006; Stockey et al., 2006; Vavrek et al., 2006; Rothwell et al., 2014) and
117 numerous gymnosperms (Stockey and Wiebe, 2008; Stockey and Rothwell, 2009; Klymiuk and
118 Stockey, 2012; Rothwell and Stockey, 2013; Rothwell et al., 2014; Atkinson et al., 2014a,
119 2014b; Ray et al., 2014; Klymiuk et al., 2015), as well as fungi (Smith et al., 2004; Bronson et
120 al., 2013) and a lichen whose thallus shows modern heteromerous organization (Matsunaga et
121 al., 2013). The Apple Bay flora is also emerging as the most diverse assemblage of fossil
122 bryophytes known in the pre-Cenozoic worldwide (Tomescu et al., 2012), with leafy and thalloid
123 liverworts, and more than twenty distinct moss morphotypes currently recognized. The mosses
124 represent pleurocarpous, polytrichaceous, and leucobryaceous types, as well as several
125 morphotypes of unresolved affinities including at least three distinct tricostate types.

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

133 SYSTEMATICS

134 *Class*—Bryopsida Rothm.

135 *Subclass*—Bryidae Engl.

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

137 *Order*—*incertae sedis*

138 **Family**—Tricostaceae Shelton, Stockey, Rothwell et Tomescu, fam. nov.

139 **Familial diagnosis**—Gametophyte plants pleurocarpous. Stems regularly to irregularly
140 pinnately branched, central conducting strand absent. Cortical cells thin-walled, hyalodermis or
141 thick-walled outer cortex lacking. Paraphyllia absent. Leaves helically arranged, with three
142 costae (tricostate) and conspicuous alar regions; laminal cells isodiametric to elongate. One to
143 few gametangia borne on lateral specialized (perigonial, perichaetial) shoots.

144 **Type genus**—*Tricosta* Shelton, Stockey, Rothwell et Tomescu, gen. nov.

145 **Generic diagnosis**—Gametophytes much-branched; leaves isophyllous, partially
146 overlapping and densely covering the stems. Branch primordia arising one or very few cells
147 above subtending leaf. Multicellular rhizoids smooth. Leaves tricostate with costae
148 symmetrically arranged, arising separately in leaf base and homogeneous in transverse section.
149 Alar regions small; laminal cells smooth, thin-walled, elongate to oval, rhombic or repand,
150 becoming isodiametric distally along lamina. Perigonia sessile on lateral branches, with one to a
151 few antheridia; perigonial leaves like vegetative leaves but smaller. Perichaetia sessile, lateral
152 along main stems, with few archegonia; perichaetial leaves different from vegetative leaves.

153 **Etymology**—*Tricosta* for the tricostate leaves.

154 **Type species**—*Tricosta plicata* Shelton, Stockey, Rothwell et Tomescu, sp. nov.

155 **Specific Diagnosis**—Gametophytes in tufts at least 20 mm high, main stems once-
156 pinnate. Branches inserted at 40-70° angles and 0.1-1.1 mm intervals. Stem diameter up to 0.2
157 mm, 10-14 cells across, epidermal cells narrower than cortical cells. Rhizoids at stem base ca.
158 24 µm in diameter. Leaves dense, 10-20 leaves per millimeter along stem; 3/8 phyllotaxis.
159 Leaves straight, with 40-55° divergence angles, ca. 2.0 mm long, 0.5 mm wide at base, up to 0.9
160 mm wide mid-leaf. Leaves ovate, margins entire, apex acute. Leaves strongly plicate

161 throughout; plications form adaxially concave longitudinal folds associated with costae. Leaf
162 lamina ca. 18 cells wide between median and lateral costae, ca. 15 cells between lateral costae
163 and leaf margin. Costae strong (ca. 0.9 of leaf length), median costa percurrent, up to 8 cells
164 wide (cells 6-9 μm diameter), composed of three layers (1-2 layers distally). Abaxial cells of
165 costa short, larger in diameter toward leaf apex. Median costa up to 55 μm wide, 30-40 μm
166 thick; lateral costae 35 μm wide, 25-40 μm thick. Alar regions up to 9 cells wide; cells
167 prominently inflated in transverse sections (diameter up to 34 μm), globose to elongate (up to 54
168 μm) in longitudinal sections. Lamina ca. 13-19 μm thick; laminal cells forming mostly oblique
169 files in base and mid-leaf; laminal cells form longitudinal files distally. Lamina cells at leaf base
170 up to 5:1 (length/width ratio) and rectangular to rhombic; mid-leaf cells 2-3:1, up to 35 μm long
171 and rhombic, repand or oval; distally, cells isodiametric and up to 23 μm diameter. Perigonial
172 branches, ca. 1 mm long overall, bear ca. 4 erect leaves ca. 0.9 mm long, similar to vegetative
173 leaves but with plications weak or absent on innermost leaves. Antheridia oblong, up to 350 μm
174 long, borne on triseriate stalks. Perichaetia with few erect leaves; perigonial leaf cells narrow
175 (ca. 4.5:1 and 40 μm long). Archegonia at least 200 μm long.

176 ***Etymology***—specific epithet *plicata* for the marked, characteristic plication of the leaves.

177 ***Holotype hic designatus***—Gametophyte shoot in rock slab UAPC-ALTA P15425 C

178 (slides Cbot series a) (Figs. 2A, D; 3; 4A, B; 6A, B; 7B, G; 8D-J; 9; 10).

179 ***Paratypes***—UAPC-ALTA P13029 Dtop (Fig. 6B), P13131 Dtop (Figs. 4F-H; 6A, B;
180 8A), P13256 Cbot (Fig. 5), P13957 A (Figs. 2B, C, E, F), P13957 Btop (Figs. 1; 4D; 6A; 7H, I;
181 8C, K, L; 11), P15422 A (Fig. 7A, C-E), P16435 Ctop (Figs. 4C, E; 7F; 8B).

182 ***Locality***—Apple Bay, Quatsino Sound, northern Vancouver Island, British Columbia
183 (50°36'21" N, 127°39'25" W; UTM 9U WG 951068).

207 in shape (Figs. 2B, C). Stems occasionally bear one to a few narrow cells (5-12 μm in diameter)
208 near the center but show no clear organization into a central conducting strand (Fig. 2C).
209 Longitudinal sections show fusiform cortical cells 57-75 μm long and up to 18-23 μm wide
210 (Figs. 2E, F). Epidermal cells are 35-60 μm long.

211 Vegetative shoot tips are incompletely preserved and show variation in preservation. The
212 tips exhibit either large cells, faint in color (Figs. 4A, B), or small cells, darker in color (Fig. 4C)
213 – the different colors may indicate different states of decomposition. Some of the shoots show
214 leaf primordia (Fig. 4C) and branch primordia (Figs. 4D, E). Branch primordia occur in leaf
215 axils, separated by at least one cell from their subtending leaf, and slightly sunken in the stem
216 tissue. They are dome-shaped, up to 60 μm wide and 40 μm tall. Each branch primordium is
217 covered by at least one over-arching scale-like structure (Figs. 4D, E). Preservation precludes
218 resolving the origin of these structures, i.e. whether the scale-like structures are derived from the
219 delicate primordium tissue or the epidermis of the surrounding stem, i.e., either a “scale leaf” or
220 “pseudoparaphyllum” origin, respectively – *sensu* Newton and De Luna (1999). The branch
221 primordia are bordered by a palisade of radially arranged cells with circular to wedge shapes (up
222 to 10 x 24 μm) in longitudinal sections (Figs. 4D, E).

223 One specimen represents the base of a small tuft (i.e., several shoots originating from a
224 small number of branching stems) covered in rhizoids (Fig. 5A). The rhizoids, densely arranged,
225 are multicellular, with characteristic oblique end-walls (Figs. 5B, C), diameters of 17-30 μm , and
226 extend up to 700 μm from the stems. Branched rhizoids were not observed.

227 *Tricosta plicata* is isophyllous and leaves are partially overlapping, densely covering the
228 stems, with ca. 9 leaves mm^{-1} in proximal regions of the shoots, and up to 23 leaves mm^{-1}
229 distally (e.g., Fig. 2A). Phyllotaxis is helical, following a 3/8 phyllotactic ratio. Leaves are erect

230 with divergence angles of 40-55° or wider where they subtend branches (Fig. 2A). Paraphyllia
231 were not observed.

232 ***Leaf morphology and anatomy***—In terms of overall shape, the leaves are symmetrical,
233 ovate, have entire margins, and are broadly attached to the stems (Figs. 6; 4F, G). The leaves are
234 ca. 0.5 mm wide at the base, reaching a maximum width of 0.9 mm and length of 2.1 mm.
235 Incomplete preservation of leaf tips permits only close approximation of total leaf length. Leaf
236 apices, when preserved, are acute (Figs. 8K, L).

237 Leaves are unistratose, strongly plicate, and tricostate (Figs. 4F-H; 6; 7A, B). Plication
238 forms three adaxially concave longitudinal folds, each associated with a costa. The median fold
239 and costa extend from the leaf base into the apex (i.e., percurrent), whereas the two lateral folds
240 and costae are shorter, extending from the leaf base to somewhere below the apex (i.e.,
241 attenuated) (Figs. 8K, L). At the widest point, the lamina is ca. 18 cells wide between the
242 median and lateral costae and ca. 15 cells between the lateral costae and leaf margin (Fig. 6).
243 Median costae end apically within 4-5 cells from the leaf margin while lateral costae end 3-4
244 cells from the margin (Fig. 6). The three costae of a leaf originate separately and slightly below
245 the level of leaf divergence (Figs. 4F, G). Leaf margins are unistratose and gently recurved
246 (curved abaxially) throughout (Fig. 6).

247 Median costae are ca. 55 µm wide and 27-42 µm thick in the basal half of the leaf, while
248 lateral costae are ca. 35 µm wide and 25-42 µm thick (e.g., Figs. 7C-E). Costae are tristratose at
249 the base, becoming bistratose in the upper half of the leaf (e.g., Figs. 4H; 6; 7A, B). Costae
250 consist of cylindrical elongate cells which form three layers: adaxial, median and abaxial (Figs.
251 7C-E). In paradermal and longitudinal sections, costal cells are 40-138 µm long, with one or
252 both ends tapered (Figs. 7F-G). Adaxial and median costa layers are up to six cells wide basally,

253 becoming one to two cells wide apically, with cells 8-16 μm in diameter. The abaxial layer is up
254 to eight cells wide basally (cells 6-9 μm in diameter; Fig. 7C), and just one or two cells wide
255 distally (cells up to 23 μm in diameter; Fig. 7B).

256 Prominent alar regions are present at the leaf base corners (Figs. 4H; 6; 7A, H, I; 8A-D).
257 They are up to nine cells wide and five cells tall. Alar cells are inflated in transverse sections
258 (e.g., Figs. 7I; 8A), ca. 15-34 μm wide, up to 54 μm long, and globose to elongate in paradermal
259 and longitudinal sections (e.g., Figs. 8B, D). Laminal cells (Figs. 6; 8E-L) are 13-19 μm thick
260 throughout. Toward leaf bases they have a length/width ratio of up to 5:1 and are ca. 40 μm long
261 (up to 62 μm) with elongate and rectangular to rhombic shapes. In the mid-leaf, cells are ca. 2-
262 3:1 and ca. 25 μm long (up to 35 μm) with mostly rhombic or oval shapes. In the distal half of
263 the leaf, cells become isodiametric, with diameters of 10-23 μm . Laminal cells adjacent to the
264 costae are comparable in size to neighboring laminal cells and have various, typically elongate
265 shapes: rhombic, repand, rectangular, and isodiametric (Figs. 6; 7G). Throughout the basal half
266 of the leaf, laminal cells typically form oblique files, whereas longitudinal files (of isodiametric
267 cells) are typical in the distal leaf half (Fig. 6). Walls of laminal cells are smooth and thin (ca.
268 1.0 μm thick; Fig. 8E).

269 *Specialized branches*—At least two specimens exhibit perigonial branches. One of these
270 is an extensively branched gametophyte with diminutive perigonial shoots borne apically or
271 laterally on nearly all branches (Figs. 3; 2A; 9). Perigonial axes are 115-200 μm long, 95-115
272 μm thick, and bear ca. 4 leaves (Figs. 10A-C). The perigonial leaves are erect or spreading and
273 anatomically similar to cauline leaves, except for a smaller size (e.g., lengths ca. 0.9 mm),
274 weaker plications, and weaker costae in innermost perigonial leaves (Figs. 10A, F). All
275 perigonial axes bear one antheridium at their tip (Figs. 10B, C). The antheridia are oblong (up to

276 350 μm long and 150 μm wide; Fig. 10C) and borne on triseriate stalks (145-150 μm long and
277 44-50 μm thick; Figs. 10B-E). The stalks are ca. 10-14 cells tall (Fig. 10D). Antheridial jackets
278 are composed of narrow (7-8 μm) cells showing irregular shapes in paradermal sections (Fig.
279 10G). Paraphyses and sperm cells were not observed.

280 At least three shoots bear perichaetial branches (Fig. 11). These specialized branches are
281 extremely short and borne laterally along main stems (Figs. 11A, B) which occur near the
282 periphery of an extensively branched gametophyte tuft (Fig. 1). The numerous other shoot tips
283 of the tuft are vegetative, incompletely preserved, or occupied by perithecioid fungal fruiting
284 bodies. The perichaetia terminate short, bud-like branches that are constricted at the base where
285 they attach to the main stem (Fig. 11A); the stem itself shows no change in diameter where the
286 perichaetial branch is attached. Perichaetia consist of few densely arranged, straight and erect
287 leaves which are crowded from their bases to near the apices (Figs. 11A-C). The leaves are
288 composed of narrow cells (up to 4.5:1 and ca. 40 μm long mid-leaf) with rectangular or rhombic
289 shapes throughout the lower half of the leaf (Figs. 11C, D). Perichaetial leaf apices were not
290 observed. The branch tips are conic (Fig. 11D) or narrowly dome-shaped (Fig. 11G) and bear a
291 small number of pale-colored archegonia (Figs. 11C, D, G). The archegonia are at least 200 μm
292 long, with a venter up to 50 μm across (Figs. 11F), and lack a distinct stalk (e.g., Figs. 11D, G).
293 In one specimen seen in oblique-longitudinal section (Fig. 11E, F), the neck canal is seen at the
294 center, with a single layer of neck cells and few layers of delicate venter tissue (Fig. 11F).

295 DISCUSSION

296 *The tricostate condition*—The costa (also termed midrib or nerve) is a multistratose
297 region of the leaf forming a longitudinal band that is anatomically different from the rest of the
298 lamina. Most moss leaves bear a single costa, which varies greatly in anatomy and morphology

309 among taxa (Goffinet et al., 2009). The condition in which a costa is divided at the base or along
310 its length (e.g., Goffinet et al., 2009) is treated as a single “forked” costa, which makes sense
311 from a developmental standpoint. Whereas ecostate mosses (mosses that lack costae or have
312 costae of insignificant length) are found among diverse lineages (e.g., *Sphagnum* L., *Buxbaumia*
313 Hedw., *Erpodium* Brid., *Pleurophascum* Lindb., *Hedwigia* Beauv.), mosses bearing multiple
314 costae per leaf (pluricostate or multicostate) are typically found among pleurocarpous taxa (e.g.,
315 *Thamniopsis* M. Fleisch., *Antitrichia* Brid., *Neckera* Hedw.; Goffinet et al., 2009). Extant
316 pluricostate mosses typically bear two short costae per leaf and instances of two strong costae
317 (e.g., some Hookerales) or more than three costae are rare (e.g., *Antitrichia*, which features a
318 median costa and a variable number of shorter accessory costae; e.g., Lawton, 1971). None of
319 these pluricostate conditions conforms to the tricostate condition of *Tricosta plicata*, in which
320 three strong costae originate independently at the leaf base and extend well beyond the midleaf.
321 In this context, the tricostate condition present in both *T. plicata* and the Mesozoic genus
Tricostium clearly sets these species apart from all other living and extinct mosses.

322 ***Tricostate analogues in extant mosses***—Although no mosses with three strong costae
323 are recognized in modern floras, a few extant mosses exhibit multilayered bands of cells
324 *additional* to the median costa that can be morphologically similar to lateral costae: (1)
325 multistratose longitudinal thickenings (or multistratose “streaks”) composed of cells more or less
326 similar to those of the lamina; and (2) multistratose intramarginal limbidia (intramarginal borders
327 or teniolae), which are bands of cells running parallel with and internal to the leaf margin by 1-3
328 cells. It is important to note that none of the rare studies of leaf development in mosses (e.g.,
329 Frey, 1970) has addressed the homology of multistratose structures of the lamina and we can
330 only base comparisons on anatomy.

322 Multistratose thickenings similar to costae are seen in *Coscinodon arctolimnius* Steere
323 and *C. cribrosus* Spruce (Grimmiaceae), in which leaves bear a median costa and two lateral
324 multistratose thickenings that run along leaf plications (Hastings and Deguchi, 1997). These
325 thickenings consist of cells similar in anatomy to those of the costa. While the multistratose
326 thickenings of *Coscinodon* Spreng. are comparable to costae in featuring elongated cells, costae
327 and multistratose thickenings are probably developmentally different as suggested by: (1) the
328 fact that cells in the streaks are shorter than those of the median costa; (2) irregular width,
329 thickness, and position of the streaks on the leaf; and (3) an absence of cell differentiation in the
330 streaks similar to that seen in the costa (i.e., stereids are present in the costae and not in the
331 streaks).

332 Multistratose intramarginal limbidia are seen in a few genera – those of *Calymperes* Sw.,
333 *Teniolophora* W.D. Reese, and *Limbella* Müll. Hal. (e.g., Gradstein et al., 2001) show the closest
334 apparent similarity to the tricostate condition of *T. plicata*. In *Calymperes* and *Teniolophora*, the
335 cross-sectional anatomy of limbidia is simpler than that of the costa, suggesting different
336 developmental origins of the two types of structures. In *Limbella tricostata* Bartr. (= *Sciaromium*
337 *tricostatum* Mitt.) the intramarginal limbidia have cross-sectional anatomy similar to that of the
338 costa (e.g., Lawton, 1971). Although among extant mosses the intramarginal limbidia of
339 *Limbella* are most similar to the lateral costae of *Tricosta*, these limbidia are much closer to the
340 leaf margin (only one to two cells away; e.g., Lawton, 1971) than the costae of *Tricosta* (with
341 leaf margins 10-15 cells wide).

342 Overall, multilayered structures of the lamina known in extant mosses that approach the
343 tricostate condition are anatomically different from, and probably not homologous to costae, as
344 discussed above. This suggests that extant moss diversity does not include any structures

345 equivalent to the lateral costae of *Tricosta*.

346 ***Taxonomic placement of Tricosta plicata gen. et sp. nov.***

347 *Justification for a new genus*—Mosses with tricostate leaves have been previously
348 reported only from Mesozoic (Triassic to Early Cretaceous) rocks in Russia and Mongolia
349 (potentially extending into the Permian; Ignatov and Shcherbakov, 2011b), where they are
350 preserved as compressions (Krassilov, 1973; Ignatov and Shcherbakov, 2011a, 2011b). These
351 mosses have been assigned to the genus *Tricostium*, with three species: *Tricostium triassicum*
352 Ignatov et Shcherbakov, *T. papillosum* Krassilov, and *T. longifolium* Ignatov et Shcherbakov.
353 The genus *Tricostium* is diagnosed as having partially overlapping, flat, unistratose leaves with
354 three costae (Krassilov, 1973).

355 The unique nature of three strong costae per leaf suggests a close relationship among all
356 tricostate mosses. However, several characters differentiate *Tricosta plicata* from the genus
357 *Tricostium* (Table 1), indicating that it represents a new genus. Aside from the tricostate leaves,
358 *Tricosta plicata* is similar to *Tricostium* only in terms of leaf divergence angles (ca. 40 – 45°),
359 leaf width (ca. 1.0 mm), and in having strong costae, and short laminal cells (Table 1). Of the
360 three species of *Tricostium*, *T. papillosum* is most similar to *Tricosta plicata*, comparing
361 favorably in leaf shape and length, and the width of the median costa. However, *Tricosta plicata*
362 differs from *T. papillosum* in branching angle, leaf density, leaf profile, leaf apex, laminal cell
363 arrangement, laminal cell shape, laminal cell dimensions, and leaf cell wall texture.

364 Furthermore, the difference in modes of preservation leads to a strong disparity between
365 *Tricosta* and *Tricostium* in the type and number of taxonomically informative characters, as well
366 as the degree of morphological and anatomical detail available. The compression fossils
367 assigned to *Tricostium* provide information on few characters, including leaf shape, size, angle of

368 divergence, and leaf density along the stems, as well as branching pattern (if present) and leaf
369 areolation (Table 1). As a result, *Tricostium* is defined chiefly on leaf characters, as the fossils
370 lack detail on other characters; consequently, none of the *Tricostium* species is reconstructed as a
371 whole plant. Therefore, *Tricostium* is best regarded as a morphogenus (i.e., a taxon defined
372 based only on a subset of characters of the whole plant; Bell and York, 2007) erected for moss
373 leaves displaying a tricostate condition. In contrast, *Tricosta plicata* preserves information on
374 several additional characters including branching architecture, phyllotaxis, stem diameters, stem
375 anatomy, detailed leaf anatomy from various planes of section, costal anatomy, and fertile
376 structures (perigonal and perichaetial shoots). Consequently, *Tricosta plicata* is characterized in
377 much more detail than any of the species of *Tricostium* and represents a natural taxon based on a
378 whole-plant concept for the gametophyte. Taken together, all these considerations warrant
379 placement of the Apple Bay material in the new genus, *Tricosta*.

380 *Tricosta plicata* as a *hypnanaean pleurocarp*—In a strict sense, pleurocarpy refers to the
381 production of sporophytes (thus, perichaetia with archegonia) on typically bud-like lateral
382 shoots. Recognition of pleurocarpy is complicated by the fact that in some acrocarpous mosses
383 (e.g. *Hedwigia ciliata* (Hedw.) P.Beauv.) new vegetative branches can be initiated immediately
384 below perichaetia that terminate long branches; in such cases, the new vegetative branch
385 displaces the perichaetium laterally, leading to a pseudo-pleurocarpous branching pattern
386 (Mishler and De Luna, 1991). In *T. plicata* the perichaetial branches are short, bud-like and,
387 importantly, they are attached by a constricted base to the main stem; additionally, the main stem
388 shows no constriction at the points of attachment of perichaetial branches. Together, these
389 observations indicate that the perichaetial branches are true laterals and support interpretation of
390 *T. plicata* as a true pleurocarp. Furthermore, the abundance of lateral bud-like perigonal

391 branches, a feature that suggests a similar branching pattern for the perichaetia (N.E. Bell, pers.
392 comm., 2013; L. Hedenäs, pers. comm., 2013) corroborates this interpretation.

393 Aside from the superorder Hypnanae, pleurocarpy is present in some members of the
394 rhizogoniaceous grade of lineages basal to the Hypnanae (Bell and Newton 2004), specifically of
395 the Orthodontiales, Rhizogoniales, and Aulacomniales (Bell et al., 2007). Of these groups,
396 which form a clade informally referred to as pleurocarpids (Bell et al., 2007), only the hypnanaean
397 pleurocarps (or subsets of this group) combine the set of gametophyte features documented in *T.*
398 *plicata*: (1) monopodial and much-branched (\pm pinnate) primary stems; (2) pluricostate, (3)
399 homocostate, (4) and strongly plicate leaves; (5) leaf cells elongate and rhombic at mid leaf, with
400 (6) thin walls, and (7) arranged in oblique files; (8) the presence of well-differentiated alar
401 regions; and (9) the absence of a central conducting strand in the stems (e.g., Lawton, 1971; Vitt,
402 1982; 1984; Hedenäs, 1994; La Farge-England, 1996; Newton and De Luna, 1999; Ignatov and
403 Shcherbakov, 2007; Newton, 2007; Goffinet et al., 2009). While none of these characters
404 considered individually is exclusively diagnostic of the Hypnanae, they each occur only
405 sporadically outside of this group, and are not known to occur in combination in any extant non-
406 hypnanaean.

407 Within the hypnanae (the clade comprising the orders Hypnodenrales, Ptychomniales,
408 Hookeriales and Hypnales), homogenous costae characterize only the clade consisting of the
409 Ptychomniales + Hookeriales + Hypnales [= the homocostate pleurocarp clade of Bell et al.
410 (2007)]. Consequently, the combination of gametophyte traits of *Tricosta* supports placement in
411 superorder Hypnanae and suggests that, within this superorder, *Tricosta* could be a member of
412 the homocostate pleurocarp clade.

413 *Justification for a new hypnanaean family*— Among the homocostate pleurocarps, the

414 Ptychomniales often have plicate leaves, while some Hookeriales are bicostate in a similar
415 manner to the way in which *Tricosta* is tricostrate. Based on the Early Cretaceous age and the
416 combination of characters of *Tricosta*, one could speculate that the tricostrate-plicate condition in
417 this fossil was ancestral to both the plicate (but sometimes ecostate) state found in many
418 Ptychomniales and the bicostate (but non-plicate) condition found in some Hookeriales.

419 When compared to individual hypnanaean families, *Tricosta* is most similar to the
420 Pilotrichaceae (Hookeriales) and families of the Hypnales (Table 2). The vast majority of
421 pleurocarp diversity belongs to the Hypnales, which comprises more than 40 families and 400
422 genera (Goffinet et al., 2009). There are numerous families within this group that have several
423 conspicuous traits in common with *Tricosta plicata* e.g., monopodial and pinnate branching,
424 absence of paraphyllia, lack of a conducting strand, helically arranged leaves, conspicuous alar
425 regions, and laminal cell morphology (Lawton, 1971; Vitt, 1982; Chiang, 1995; Gradstein et al.,
426 2001; Goffinet et al., 2009; Eckel, 2011; Ramsay, 2012a; Ramsay, 2012b). Families exhibiting
427 some combination of these traits are included in Table 2. Of these families, Amblystegiaceae,
428 Regmatodontaceae, Hypnaceae, and Rhytidiaceae are most similar to *Tricosta* (Table 2).
429 However, each of these families exhibits significant differences from *Tricosta* (Table 2).
430 Additional differences not listed in Table 2 include: stem anatomy (in Pilotrichaceae: a few outer
431 cortex layers with narrow, thick-walled cells and, typically, a hyalodermis) and isodiametric
432 distal leaf cells, present in *Tricosta* but not known in any of the families listed above. Together,
433 the differences suggest that none of these families is a good placement for *Tricosta* and, along
434 with the unique tricostrate condition, warrant erection of a new family, Tricostaceae.

435 ***Pleurocarpous mosses in the pre-Cenozoic fossil record***—Few pre-Cenozoic mosses
436 have been discussed in terms of putative pleurocarpy. In such discussions, pleurocarpy has been

437 suggested based on characters that are not exclusively diagnostic of this condition when
438 considered independently (e.g., much-branched gametophytes, equivocal reproductive
439 structures). *Uskatia* Neuburg, described from the Permian of Russia, has been compared to
440 pleurocarps by Oostendorp (1987), based on abundantly branched pinnate stems with small
441 leaves. However, Ignatov and Shcherbakov (2007) have suggested that the genus is part of a
442 different group, due to the presence of leaves attached to the stem only by their costa, a character
443 unknown in any living mosses. *Capimirinus riopretensis* Christiano De Souza, Ricardi Branco
444 et Leon Vargas (2012), known from Permian rocks of Brazil, shows sparse dichotomous
445 branching, leaves ca. 1.4 x 0.5 mm, and a putative sporophyte attached to a short lateral shoot.
446 However the sporophytic nature of this structure is equivocal because of its unusually small
447 dimensions. Because of the uncertain nature of this structure and the lack of other informative
448 characters, the placement of *Capimirinus riopretensis* among pleurocarpous mosses is uncertain.

449 *Palaeodichelyma sinitzae* Ignatov et Shcherbakov (2007), described from the Jurassic
450 (Lower Cretaceous?) of Russia, has characters that suggest pleurocarpy, such as lateral bud-like
451 structures. This species exhibits traits seen in the pleurocarpous family Fontinalaceae: strong
452 costae, keeled leaves, tristichous phyllotaxis, and elongate laminal cells (Ignatov and
453 Shcherbakov, 2007). However, pleurocarpy of *Palaeodichelyma* is conjectural, because the
454 exact nature of its lateral bud-like structures is not known, and the laminal cells have transverse
455 end-walls, which are rare among the pleurocarpous mosses.

456 *Bryokhutuliinia* Ignatov, preserved as compressions in the Jurassic (Lower Cretaceous?)
457 of Russia and Mongolia (Ignatov and Shcherbakov, 2007, 2011a; Ignatov et al., 2011), has
458 pinnately branched shoots and bud- or rosette-like structures interpreted as gametangial
459 branches. Although pinnate branching is indicative of pleurocarpy and some of the leaf traits

460 suggest Hookerian affinities (e.g., ecostate and complanate leaves; Ignatov and Shcherbakov,
461 2007), additional evidence is needed to unequivocally establish pleurocarpous affinities for this
462 moss. This is also the case for *Vetiplanaxis*, described from Cretaceous Burmese amber. This
463 fossil moss compares favorably to the pleurocarpous Hypnodendrales based on branching
464 patterns and laminal cell morphology (Hedenäs et al., 2014), but additional evidence is needed to
465 support assignment to the group.

466 Overall, among the pre-Cenozoic mosses, *Palaeodichelyma*, *Bryokhutuliinia* and
467 *Vetiplanaxis* compare most favorably to extant pleurocarps (e.g., Hedenäs et al., 2014).
468 However, in these taxa, pleurocarpy is suggested based on only a few characters encountered in
469 extant pleurocarpous mosses (e.g., general appearance, pinnate branching), rather than on a well-
470 defined, extensive set of diagnostic criteria. In this context, the suite of traits listed above in
471 support of the systematic affinities of *Tricosta plicata* provides the strongest evidence to date for
472 pleurocarpy and, more specifically, for placement in the Hypnanae of any pre-Cenozoic moss.

473 ***Gametangia in the pre-Cenozoic fossil record***—The only previously described fossil
474 bryophyte with preserved archegonia is the leafy liverwort *Naiadita* Brodie from the Triassic of
475 England (Harris, 1938). The fossil record of antheridia borne on free-living gametophytes is
476 sparse. A few Early Devonian vascular plant gametophytes from the Rhynie chert (*Remyophyton*
477 *delicatum* Kerp, Trewin et Hass, *Kidstonophyton discoides* Remy et Hass, *Lyonophyton*
478 *rhyniensis* Remy et Remy) show well preserved antheridia (Taylor et al., 2009). *Eopolytrichum*
479 *antiquum* (Konopka et al., 1997) is the only previously known instance of preservation of
480 antheridia in the moss fossil record. Aside from that, a very small number of equivocal splash
481 cups or perigonia are known (Townrow, 1959; Ignatov and Shcherbakov, 2007; Christiano De
482 Souza et al., 2012). The antheridia and archegonia of *Tricosta plicata* are, thus, a welcome

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697 **Table 1.** Summary of *Tricosta plicata* gen. et sp. nov. defining characters and a comparison with species of *Tricostium*.

	<i>Tricosta plicata</i>	<i>Tricostium longifolium</i>	<i>Tricostium papillosum</i>	<i>Tricostium triassicum</i>
Stem length (min.)	22 mm	10 mm	3.9 mm	?
Branch length (min.)	500 µm	5.5-7.5 mm	1.3 mm	?
Distance between branches (min.)	480 µm	5.0 mm	?	?
Stem diameter	0.2 mm	ca. 0.3 mm	?	?
Branching angle	(41)-55-(75°)	ca. 25-35(60°)	ca. 43°	?
Density of foliation	dense, (11)-18-(23) leaves mm ⁻¹	sparse; ca. 1.6 leaves mm ⁻¹	dense, ca. 3-5 leaves mm ⁻¹	?
Leaf divergence	erect-spreading (38)-45-(55°)	15-45° at base; distal half recurved	patent (ca. 25-40°)	?
Leaf orientation	straight	recurved	straight	?
Leaf shape	ovate	lanceolate	ovate (to narrowly ovate)	narrowly lanceolate (?or oblong)
Leaf concavity	plicate	some keeled	flat (?slightly undulate)	flat (?to concave)
Leaf margin	entire	?	serrate distally	entire
Leaf length	ca. 2.0 mm	4-6 mm	1.2-1.8 mm	4-5 mm
Leaf width	0.8-1.0 mm	up to 1.5 mm	ca. 0.5-1 mm	0.9 mm
Leaf apex	acute (?to acuminate)	acute	obtuse to acute	acute?
Leaf base	clasping	truncate?	clasping (?or auriculate)	truncate?
Median costa length (% of leaf length)	at least 95 (attenuated to percurrent)	at least 90	90-95 (attenuated to percurrent)	at least 80
Median costa width	ca. 54 µm	60-80 µm	ca. 50 µm	80 µm

	<i>Tricosta plicata</i>	<i>Tricostium longifolium</i>	<i>Tricostium papillosum</i>	<i>Tricostium triassicum</i>
Lateral costa length (% of leaf length)	at least 90	at least 90	70-90	at least 80
Lateral costa width	ca. 35 µm	ca. 25 µm	ca. 20-30 µm	30-40 µm
Alar region	conspicuous; cells inflated	?	?	?
Laminal cell arrangement	oblique files near mid-leaf; longitudinal files in distal half	?oblique files	longitudinal files	longitudinal files
Laminal cell shape	rhombic, repand, oval to isodiametric	isodiametric (?rounded or polygonal)	polygonal, isodiametric	quadrate to short rectangular
Laminal cell size	up to 5:1 (ca. 40 µm long) basally; 2-3:1 at mid-leaf (ca. 25 µm long); isodiametric up to 23 µm distally	13-17 µm	15-18 µm	13-16 µm wide
Leaf cell wall thickenings	absent	?	?thickened corners	?
Laminal cell surface texture	smooth	?	pluripapillate (8-10 papillae per cell)	?

699 **Table 1.** Comparison of *Tricosta plicata* gen. et sp. nov. to some monopodially branched pleurocarpous mosses^{2,3}.

	Pilotrichaceae	Amblystegiaceae	Regmatodontaceae	Hypnaceae	Rhytidiaceae	Pylaisiadelphaceae	Sematophyllaceae	<i>Tricosta plicata</i>
Branching	irregular to pinnate	irregular to subpinnate	irregular to subpinnate	pinnate	pinnate	pinnate	irregular to pinnate	irregular to pinnate
Stem conducting strand	absent	usually present	weak	present	narrow	usually absent	absent	absent
Paraphyllia	absent	occasional	absent	usually absent	absent	?absent	absent	absent
Leaf orientation	straight	straight to falcate-secund	straight	often falcate or falcate-secund	often \pm secund	straight; few falcate	occasionally secund, rarely falcate-secund	straight
Leaf surface topography	some concave	rarely plicate; some concave	some concave	often concave (or plicate)	plicate, rugose	some concave	concave	strongly plicate
Costa(e)	strong, double	mostly single, often variable	single	short and double or absent	single, strong	short and double or none	short and double or none	three, strong
Laminal cell shape	various	short to linear	short to elongate	mostly linear	linear	mostly linear	mostly linear	short to elongate
Laminal cell surface and walls	smooth or papillose; porose or not	smooth or rarely prorulose, some mammillose or papillose	smooth	smooth or papillose	strongly porose, prorulose	smooth, sometimes papillose	smooth or papillose	smooth
Alar cells	undifferentiated	not to strongly differentiated	not or barely differentiated	usually well-differentiated, quadrate to inflated	well-differentiated	few, quadrate, usually not inflated	well-differentiated; basal 1-2 rows strongly inflated	few, well-differentiated, \pm inflated (rarely quadrate)

700

701 ² The classification follows Goffinet et al. (2009); Pilotrichaceae within Hookeriales; all other families within Hypnales.

702 ³ Based on Lawton (1971), Vitt (1982), Chiang (1995), Gradstein et al. (2001), Goffinet et al. (2009), Eckel (2011), Ramsay (2012a, b).

703 **Figure 1.** *Tricosta plicata* gen. et sp. nov. (A) Tuft of gametophytes seen in various planes
704 of section. (B) Same image as A, with stems traced for clarity; scale bar = 2 mm; P13957
705 Btop #16.

706

707 **Figure 2.** Habit, branching, shoot architecture, and stem anatomy of *Tricosta plicata* gen. et
708 sp. nov. (A) Shoot in longitudinal section; narrow arrowheads show antheridia (upper
709 arrowhead = sac; lower = stalk); all other arrowheads indicate perigonial branches; scale bar
710 = 200 μm ; P15425 C bot #38a. (B) Stems in transverse sections showing radially arranged
711 cortical cells; scale bar = 100 μm ; P13957 A #2. (C) Detail of B; note few, scattered,
712 narrow cells near stem center; scale bar = 50 μm ; P13957 A #2. (D) Composite image of
713 much-branched shoot in longitudinal section; arrowhead at far left shows vegetative branch;
714 all other arrowheads represent positions of perigonial branches; scale bar = 500 μm ; P15425
715 Cbot #56a. (E) Stem in longitudinal section; scale bar = 100 μm ; P13957 A #2. (F) Detail
716 of E showing fusiform cortical cells; scale bar = 50 μm ; P13957 A #2.

717

718 **Figure 3.** Branching architecture of *Tricosta plicata* gen. et sp. nov. reconstructed from
719 serial sections (P15425 Cbot #1a-#92a); red dots represent perigonia; broken lines at apex of
720 main stem indicate uncertain branch arrangement; other broken lines indicate saw cuts; scale
721 bar = 1 mm.

722

723 **Figure 4.** Shoot architecture and stem anatomy of *Tricosta plicata* gen. et sp. nov. (A)
724 Vegetative shoot tip in longitudinal section; scale bar = 200 μm ; P15425 Cbot #55a. (B)
725 Detail of A showing a group of faintly colored apical cells; scale bar = 50 μm ; P15425 Cbot

726 #55a. (C) Darkened shoot tip showing scale-like leaf primordium (arrowheads); scale bar =
727 50 μm . P16435 Ctop #15. (D) Branch primordium in longitudinal section; subtending leaf
728 distanced one or two cells from primordium; thick arrowhead indicates base of scale-like
729 structure surrounding primordium; note dark hypha within costa (thin arrowhead); scale bar
730 = 50 μm ; P13957 Btop #25. (E) Branch primordium in longitudinal section directly
731 subtended by leaf; thick arrowhead indicates scale-like structure; subtending leaf base
732 indicated by thin arrowhead; scale bar = 50 μm ; P16435 Ctop #14. (F) Shoot transverse
733 section showing leaf median costa (thick arrowhead) and one lateral costa (thin arrowhead)
734 attached below point of leaf divergence; scale bar = 50 μm ; P13131 Dtop #12c. (G) Serial
735 section of F just above point of leaf divergence (with the median and lateral costa,
736 arrowheads); scale bar = 50 μm ; P13131 Dtop #13c. (H) Transverse section of shoot just
737 above branching point showing unistratose and strongly plicate leaves with three costae per
738 leaf (abaxial surface of one leaf underlined; c = costa); note paradermal section of part of
739 leaf base (alar cells, arrowhead); scale bar = 100 μm ; P13131 Dtop #3c.

740

741 **Figure 5.** Rhizoids of *Tricosta plicata* gen. et sp. nov. (A) Base of gametophyte tuft
742 showing several stems in transverse section bearing rhizoids; scale bar = 200 μm ; P13256
743 Cbot #19. (B) Stem in transverse section (at left) surrounded by smooth-walled rhizoids;
744 arrowheads indicate oblique end-walls within rhizoids; scale bar = 100 μm ; P13256 Cbot
745 #36. (C) Smooth-walled rhizoids in transverse (thick arrowheads) and longitudinal
746 sections (at left); thin arrowhead indicates oblique end-wall; scale bar = 50 μm ; P13256
747 Cbot #34.

748

749 **Figure 6.** *Tricosta plicata* gen. et sp. nov. leaf model. (A) Cell morphology; note the
 750 thickened cell walls at mid-leaf (right side), representing cells whose wall outlines are
 751 followed by fungal hyphae; tracings are from nine different leaves: a – P13131 Dtop #4c; b
 752 – P13957 Btop #52; c – P15425 Cbot #47a; d – P15425 Cbot #49a; e – P15425 Cbot #49a; f
 753 – P15425 Cbot #47a; g – P15425 Cbot #14a; h – P15425 Cbot #54a; i – P13957 Btop #157.
 754 (B) Series of leaf tracings (right) in transverse section from apex (1) to base (7) demonstrate
 755 strong plication throughout; photos (below, with leaves highlighted) correspond to serial
 756 tracings with same number; leaf sections from seven different leaves; specimen numbers
 757 correspond to serial tracings from base to apex: P13029 D #21; P 13029 D #21; P15425
 758 Cbot #26a; P15425 Cbot 22a; P13131 Dtop #3c; P15425 Cbot #16a; P15425 Cbot #11a;
 759 scale bar = 200 μm for A and B.

760

761 **Figure 7.** Leaf anatomy of *Tricosta plicata* gen. et sp. nov. (A) Shoot transverse section
 762 showing tricostate leaves with strong plications (two leaves highlighted); arrowhead
 763 indicates alar region in paradermal section; scale bar = 50 μm ; P15422 A #1. (B) Perigonial
 764 shoot in transverse section (center indicated by asterisk); innermost leaves (ca. 4) perigonial,
 765 other leaves vegetative; note protruding bistratose abaxial costa-layer (thin arrowheads);
 766 thick arrowhead indicates bundle of epiphyllous fungal hyphae; scale bar = 100 μm ; P15425
 767 Cbot #16a. (C) Leaf transverse section showing three-layered median costa (ab-, adaxial
 768 surfaces traced; arrowheads = costal layers); scale bar = 50 μm ; P15422 A #1. (D) Leaf
 769 transverse section showing three-layered median costa (below) and bi-layered lateral costa
 770 (above); scale bar = 50 μm ; P15422 A #1. (E) Leaf transverse section showing three-
 771 layered median costa (below); note alar region (above) and adjacent lateral costa

772 (arrowhead); scale bar = 50 μm ; P15422 A #1. (F) Costa in longitudinal section showing
773 linear cells with tapered (arrowhead) or transverse end-walls; scale bar = 50 μm ; P16435
774 Ctop #13. (G) Costa in paradermal section showing linear cells with tapered or transverse
775 end-walls, and juxtacostal cells (arrowheads); scale bar = 100 μm ; P15425 Cbot #54a. (H)
776 Two leaf bases in longitudinal section showing few cells (arrowheads) of two different alar
777 regions; scale bar = 50 μm ; P13957 Btop #52. (I) Alar region in transverse section;
778 arrowhead indicates adjacent lateral costa; note stem center occupied by hyphae; scale bar =
779 50 μm ; P13957 Btop #25.

780

781 **Figure 8.** Leaf anatomy of *Tricosta plicata*. (A) Shoot in transverse section showing
782 inflated alar cells of (shaded) clasping leaf base (arrowhead = median costa); scale bar = 100
783 μm ; P13131 Dtop #6c. (B) Densely foliated shoot in longitudinal section (leaf bases at left,
784 stem at right); arrowhead indicates inflated alar cell; scale bar = 50 μm ; P16435 Ctop #10.
785 (C) Cells of leaf base in paradermal section (center) and few alar cells in section (thick
786 arrowhead); thin arrowhead = lateral costa; scale bar = 50 μm ; P13957 Btop #52. (D) Alar
787 region in paradermal section; scale bar = 50 μm ; P15425 C bot #44a. (E) Leaf cells in
788 paradermal section showing thin walls indicative of the absence of fungal hyphae or
789 taphonomic alterations; scale bar = 30 μm ; P15425 Cbot #49a. (F) Leaves in paradermal
790 section showing laminal cell shapes near leaf base (lower left) and in lower half of leaf
791 (right); scale bar = 100 μm ; P15425 Cbot #47a. (G) Laminal cell shapes in distal half of
792 leaf; scale bar = 50 μm ; P15425 Cbot #49a. (H) Leaves in paradermal sections showing cell
793 shapes of mid-leaf; scale bar = 100 μm ; P15425 Cbot #49a. (I) Leaf paradermal section
794 showing cell shapes at mid-leaf; note fungi (arrowheads); scale bar = 100 μm ; P15425 Cbot

795 #48a. (J) Paradermal section showing leaf cell shapes at mid-leaf; scale bar = 100 μm ;
796 P15425 Cbot #48a. (K) Leaf apex in paradermal section; note leaf margins not shown; scale
797 bar = 50 μm ; P13957 Btop #157. (L) Detail of K showing laminal cell shapes and median
798 costa (upper arrowhead shows linear cells of adaxial costal layer; lower arrowhead shows
799 short cells of abaxial costal layer); scale bar = 50 μm ; P13957Btop #157.

800

801 **Figure 9.** *Tricosta plicata* gen. et sp. nov. Several perigonia in transverse sections
802 (asterisks), some showing antheridia (arrowheads); scale bar = 200 μm ; P15425 Cbot #13a.

803

804 **Figure 10.** Perigonia of *Tricosta plicata*. (A) Perigonial shoot in transverse section
805 showing antheridium at center and innermost perigonial leaves (arrowheads) with weak
806 costae and plication; scale bar = 100 μm ; P15425 Cbot #25a. (B) Perigonium in
807 longitudinal section showing incompletely preserved swollen axis (thick arrowhead) and
808 well-preserved antheridial stalk (thin arrowhead; note base of sac attached to stalk); scale
809 bar = 100 μm ; P15425 Cbot #38a. (C) Perigonium in longitudinal section showing
810 incompletely preserved axis (thick arrowhead, bottom), antheridial stalk (thin arrowhead),
811 and antheridial sac (between thick arrowheads); scale bar = 100 μm ; P15425 Cbot #36a.
812 (D) Detail of B showing antheridial stalk in longitudinal section; arrowhead indicates base
813 of antheridial sac; scale bar = 50 μm ; P15425 Cbot #38a. (E) Antheridial stalk in transverse
814 section; scale bar = 50 μm ; P15425 Cbot #28a. (F) Perigonium transverse section showing
815 convoluted antheridial jacket and innermost perigonial leaf; scale bar = 50 μm ; P15425 Cbot
816 #38a. (G) Antheridial jacket in longitudinal section showing irregular and narrow cell
817 shapes (e.g., inset; scale bar = 10 μm); scale bar = 50 μm ; P15425 Cbot #38a.

818

819 **Figure 11.** Perichaetia and archegonia of *Tricosta plicata* gen. et sp. nov. (A-B) Stem
820 (dashed line) and lateral perichaetial branch (arrowhead) in longitudinal section; the stem
821 that bears the perichaetial branch exits the plane of section in which the latter is seen; note
822 constricted base of perichaetial branch where it is attached to main stem; scale bars = 300
823 μm ; A, P13957 Btop #129; B, P13957 Btop #131. (C) Perichaetium in longitudinal section;
824 scale bar = 100 μm ; P13957 Btop #132. (D) Detail of C showing incompletely preserved
825 perichaetium axis and bases of archegonia (bottom); at least two archegonia shown with
826 delicate venters (v) overlapping; scale bar = 100 μm ; P13957 Btop #132. (E) Archegonium
827 diagram demonstrating plane of section (in between dashed lines) shown in F;
828 approximately to scale of F. (F) Oblique section of archegonium showing narrow neck
829 canal (c), single layer of neck cells (n) and few layers of delicate venter (v); scale bar = 20
830 μm ; P13957 Btop #121. (G) Perichaetium longitudinal section showing archegonial base
831 attached to apex of perichaetial branch; scale bar = 50 μm ; P13957 Btop #89. c = neck
832 canal; n = neck; pl = perichaetial leaf; v = venter.

Figure 1

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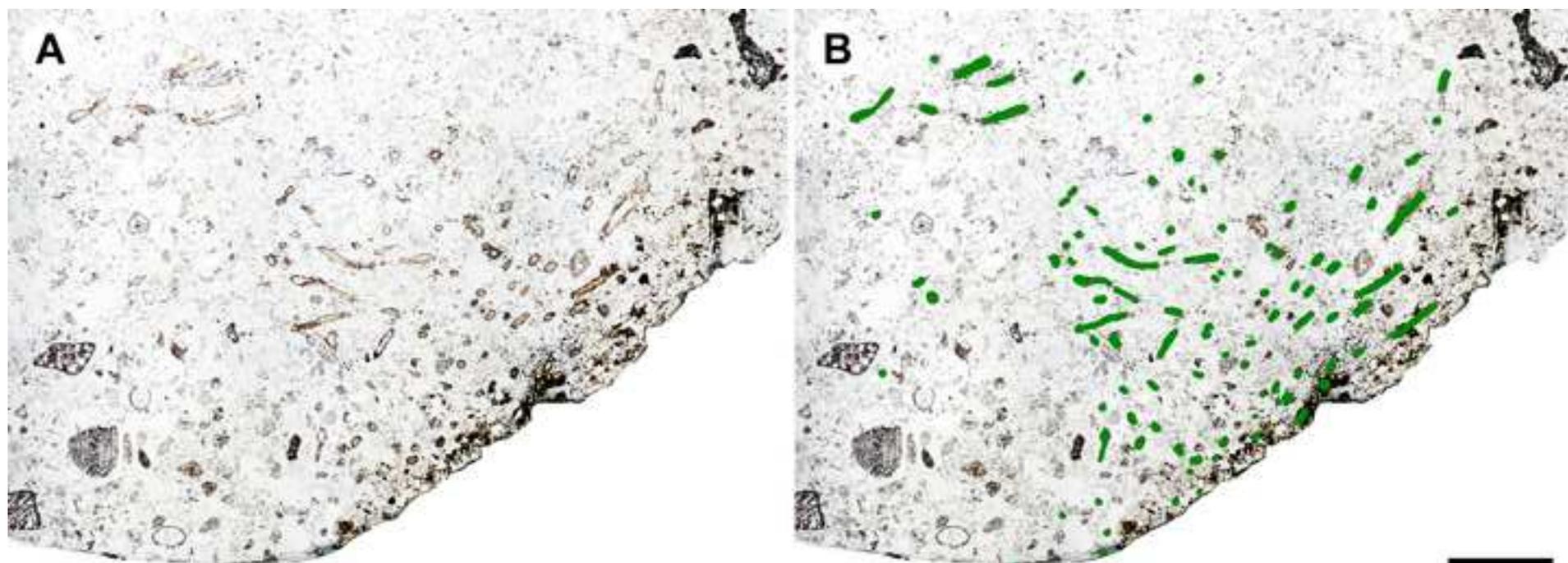


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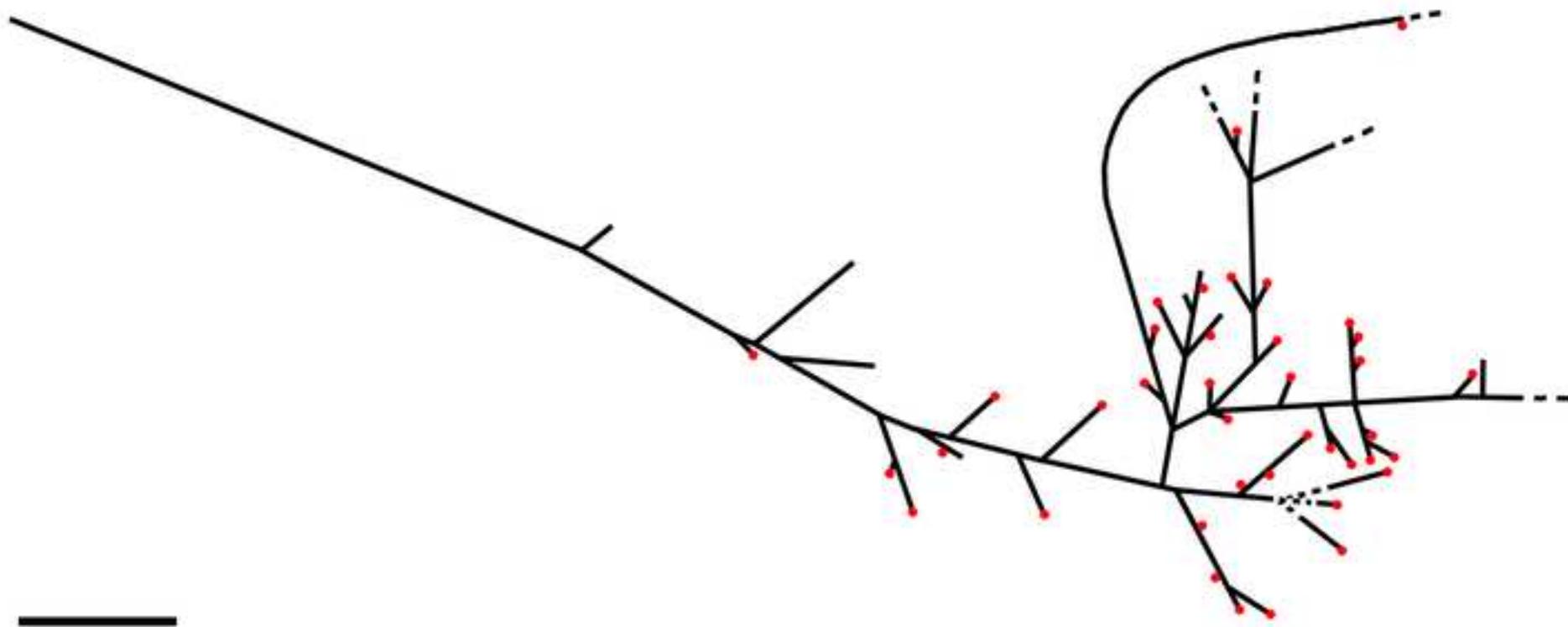


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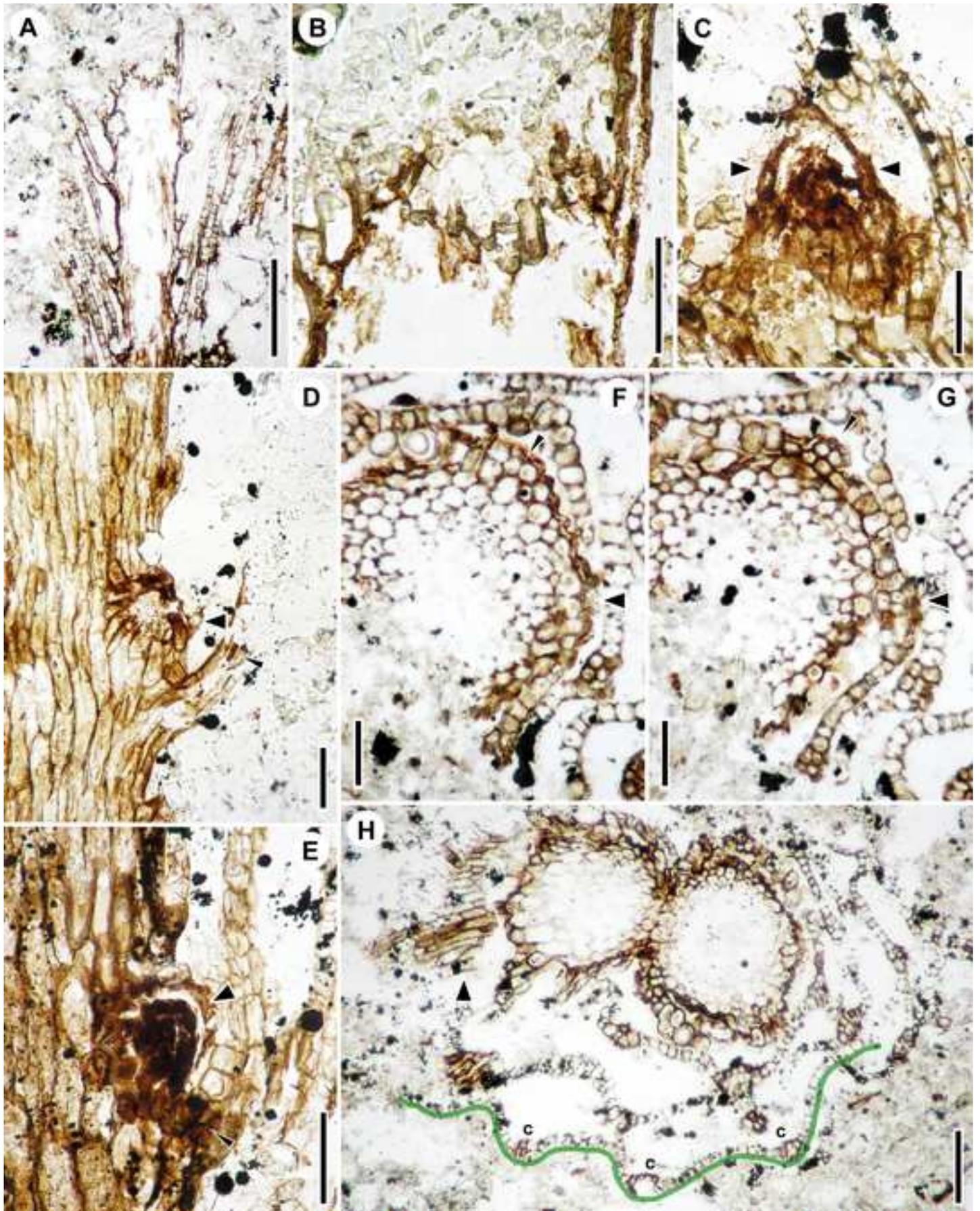


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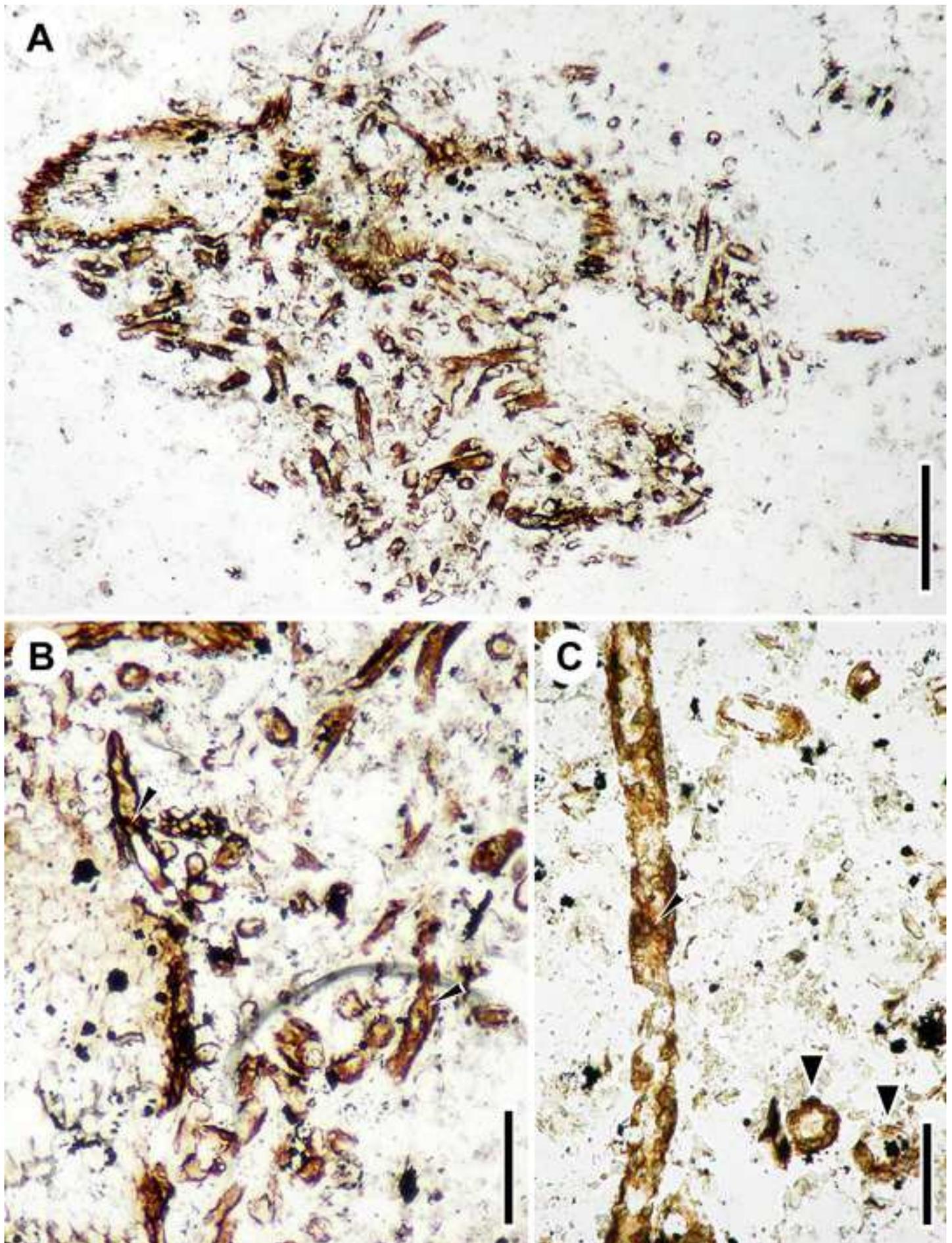


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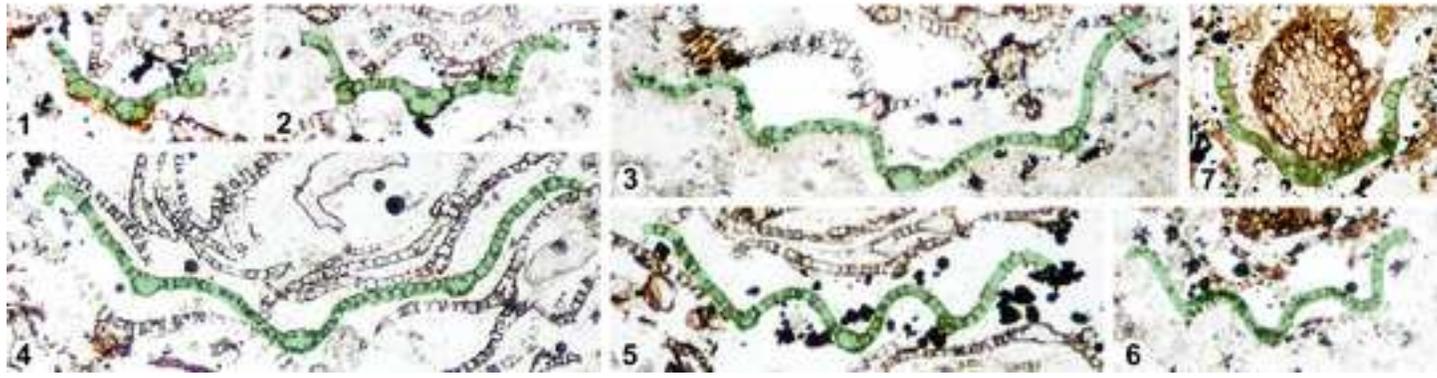
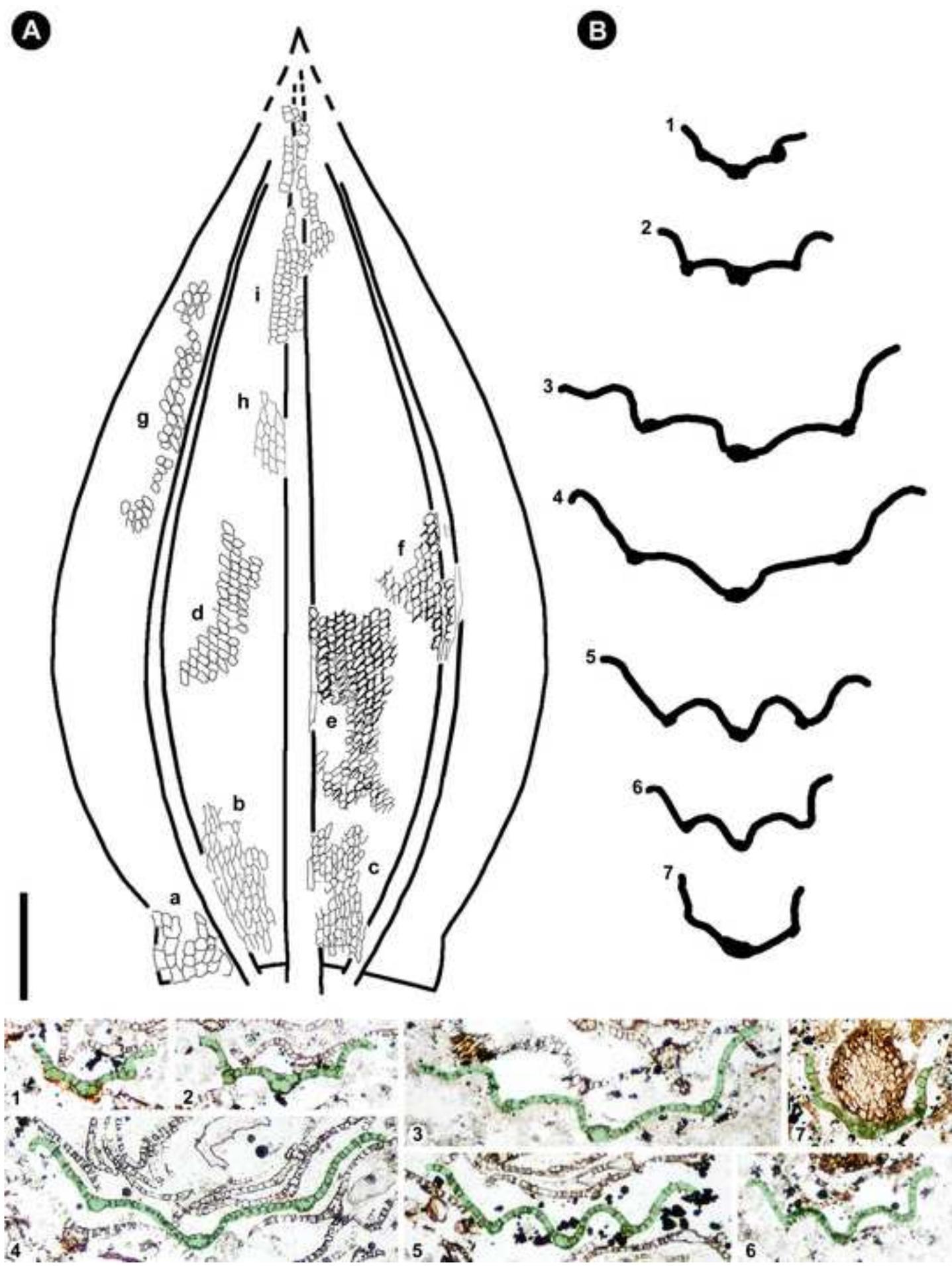


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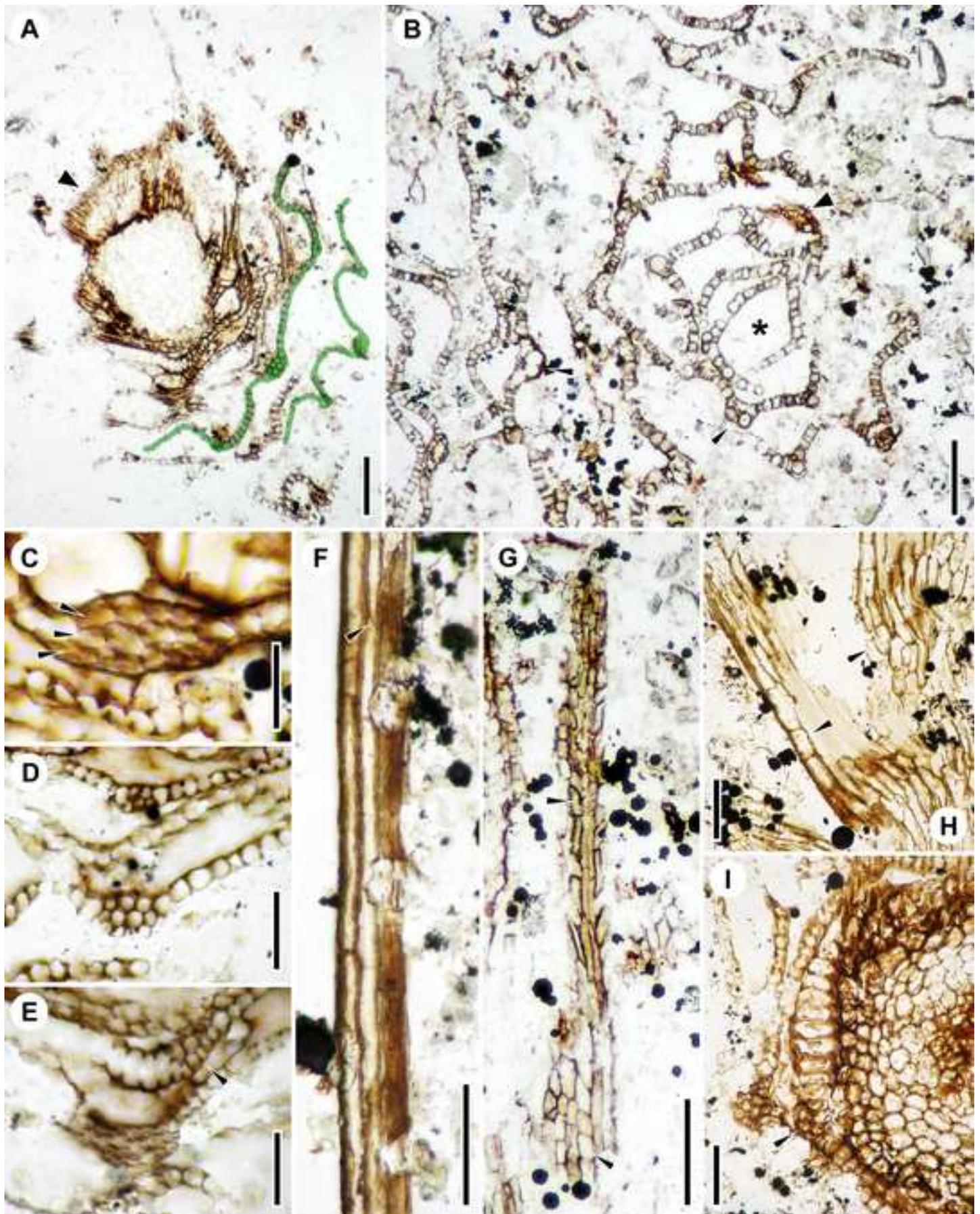


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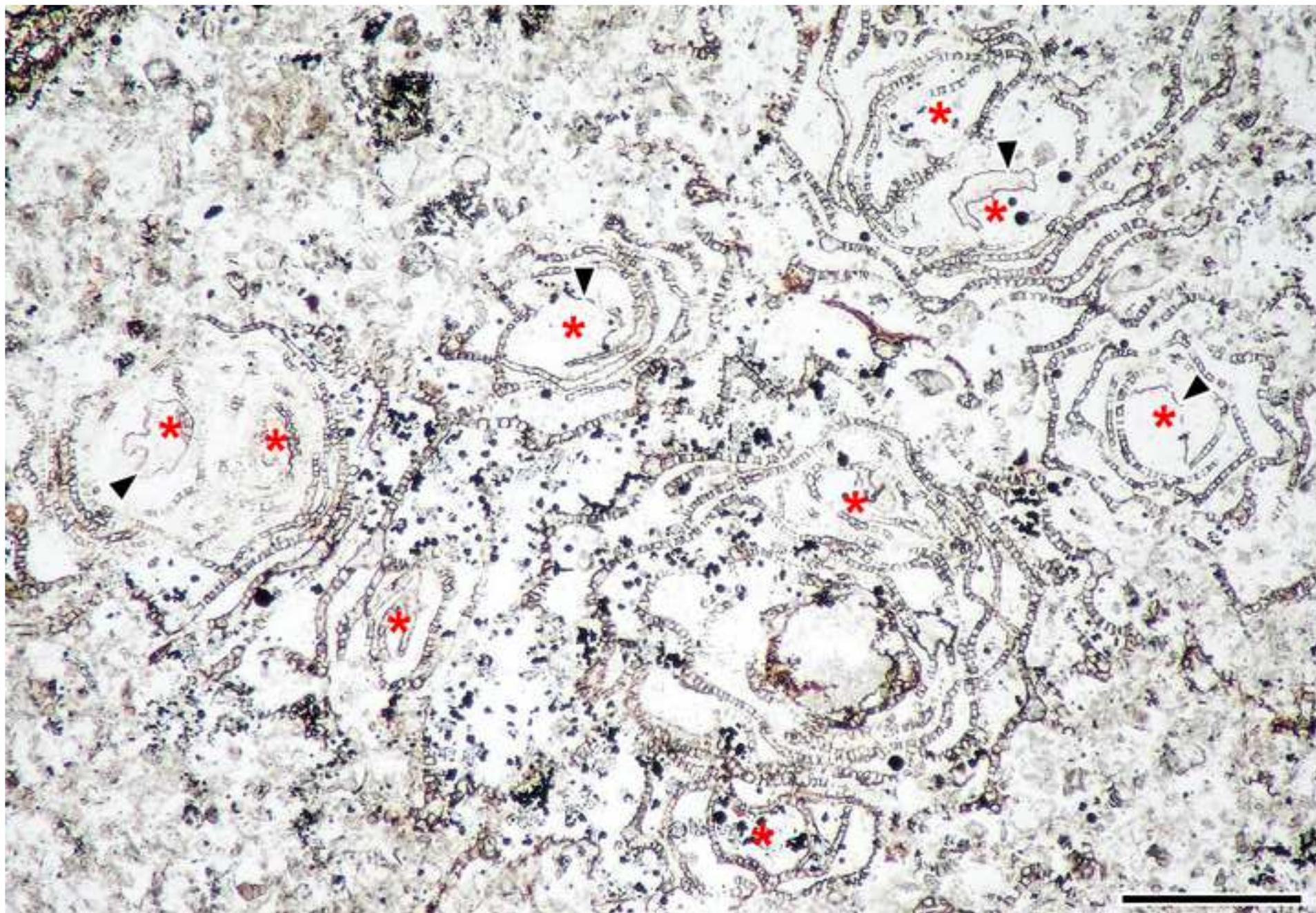
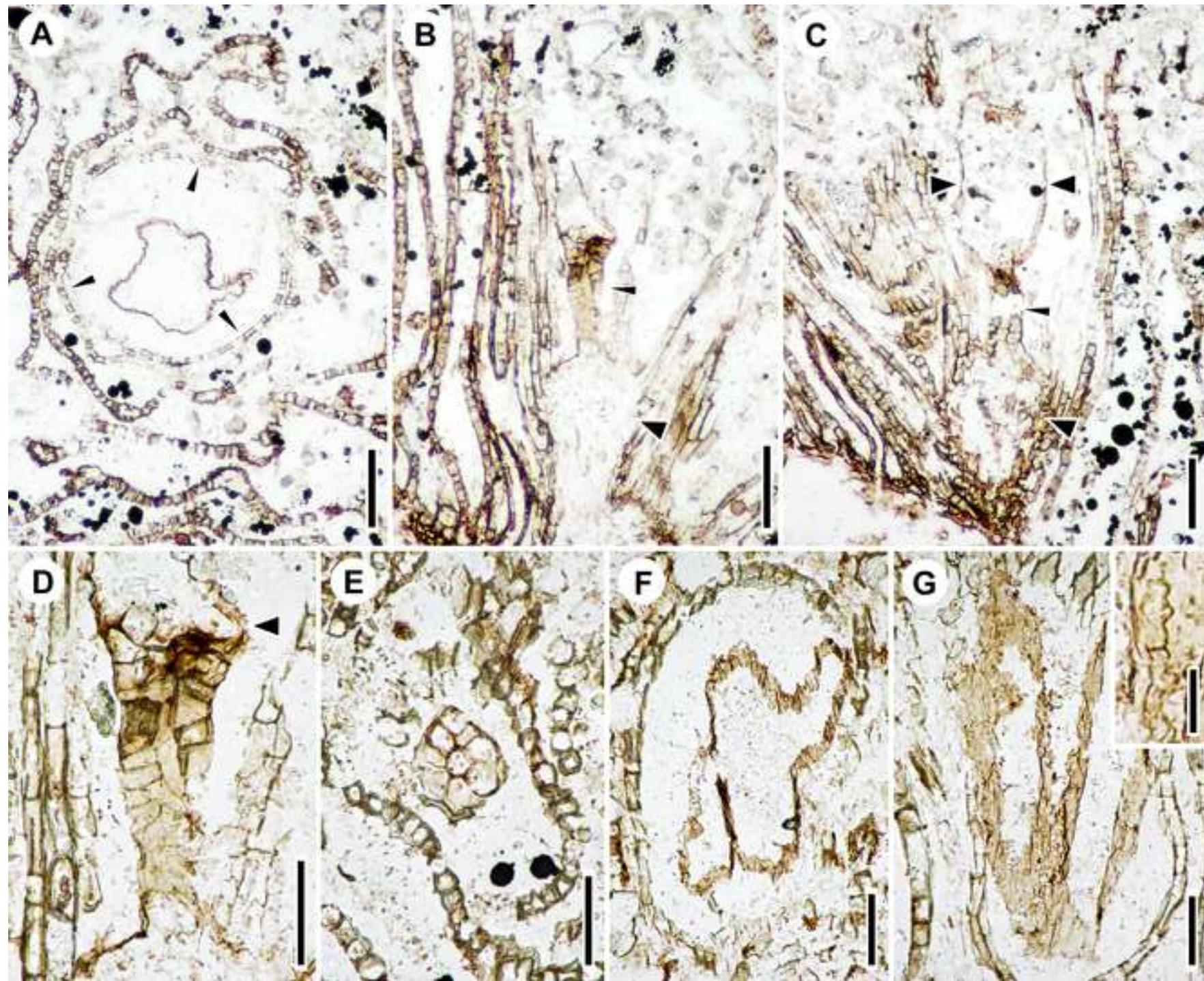


Figure 10
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Tricosta plicata Shelton, Stockey, Rothwell et Tomescu gen. et sp. nov. (Bryopsida, Hypnanae). Cross sections through the apical regions of four gametophyte stems representing branches of the same individual. The four stems, seen here on a micrograph of a cellulose acetate peel, are recognized by the concentric cycles of tricostate, plicate leaves. The branch at top left is a perigonial branch and has an antheridial sac at the center. For a measure of scale, the unistratose lamina of the leaves is 13-19 μm thick. The dark dots interspersed among the plant material are sedimentary pyrite crystals.

Tricosta is a fossil moss found in Early Cretaceous (Valanginian, ca. 136 Ma) rocks on Vancouver Island (British Columbia, Canada). The fossils are anatomically preserved by calcium carbonate permineralization, a mode of preservation considered rare, up until now, for mosses, and which allowed for detailed reconstruction of the gametophytes. The combination of features of *T. plicata* demonstrates that it is a hypnanaean pleurocarpous moss – the oldest fossil that can be unequivocally assigned to this group. Among pleurocarps, *Tricosta* represents a new family that has no living representatives and is characterized, among other features, by tricostate leaves. Tricostate leaves like those of *Tricosta* are unknown in extant mosses, but they occur in several fossil mosses (placed in the morphogenus *Tricostium* Krassilov) that span the entire Mesozoic. The discovery of *Tricosta* reveals a previously unknown slice of bryophyte diversity, whereas its similarities with *Tricostium* suggest that tricostate mosses were a diverse and widely spread group in Mesozoic bryofloras. In the context of a very sparse pre-Cenozoic moss fossil record, the fact that *T. plicata* is only the first species to be described from a very diverse fossil bryoflora preserved in exquisite anatomical detail in the Early Cretaceous of Vancouver Island, gives us hope that upon complete characterization this bryoflora will provide significant contributions to the evolutionary history of bryophytes.