# A fossil dicranid moss from the Late Cretaceous of Antarctica

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**Abstract.** An anatomically preserved moss gametophyte has been discovered in a marine carbonate concretion from the Baculites Hill locality, James Ross Island, Antarctica. The concretion is derived from the Late Cretaceous Beta Member of the Santa Marta Formation, dated as early to middle Campanian (ca. 80 Ma). The moss has actinomorphic stems with alternate branching, spiral, patent leaf arrangement and large numbers of attached rhizoids. The largest stem is 210 μm in diameter with the largest branch measuring up to 3.7 mm long and 90–100 μm wide. Most stems appear to contain a distinct conducting strand. Cross sections show that the leaves are strongly plicate with a simple D-shaped costal anatomy and unistratose laminae typically with bistratose margins. Leaves range from 650–700 μm wide and at least 700 μm long. The costa appears percurrent, 90 μm wide and 55 μm thick. Laminar cells are elongate, rhomboidal, L/W = 5:1. No ornamentation or papillae have been observed on the upper medial cells of the leaf. These fossils show leaf morphology and costal anatomy similar to several orders of acrocarpous mosses, in the Dicranidae including species of the family Rhabdoweisiaceae. While the combination of characters does not fit into any known genus, it suggests that this moss represents a fossil member of the Dicranales s.l. To date, this represents the most completely preserved moss gametophyte from Gondwana.

**Keywords.** Anatomy, Dicranidae, Rhabdoweisiaceae.

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In contrast to that of vascular plants, the bryophyte fossil record traditionally has been regarded as both sporadic and incomplete. Bryophyte fossils are most often represented by coalified compressions or impressions with little anatomical detail preserved (Tomescu et al. 2018). Recently, paleobotanical studies have revealed a small number of well-preserved moss fossils from the Permian onward that exhibit remarkably detailed information about morphology, internal anatomy, and well-preserved cuticular structure (Bippus et al. 2022; Ignatov & Maslova 2021; Tomescu et al. 2018). Such occurrences have much potential for elucidating moss systematics and evolution. The oldest known moss showing detailed internal anatomy is from siliceous permineralizations in Permian deposits of Antarctica (Smoot & Taylor 1986), with more recent examples not known until the Jurassic or Early Cretaceous (Bippus et al. 2017, 2018, 2019, 2021, 2022; Blanco-Moreno et al. 2023; Savoretti et al. 2018; Shelton et al. 2015, 2016; Tomescu et al. 2018). While mosses preserved in amber show external cellular detail and provide crucial information on extinct diversity in deep time (e.g., Feldberg et al. 2023), such specimens typically reveal little internal histology. Knowing the internal anatomy of mosses helps in identifying them to family, as minor characters at the cellular level in stems and leaves, as well as cell ornamentation, are important in moss systematics (see e.g., Crandall-Stotler & Bartholomew-Began 2007; Goffinet et al. 2009; Lüth 2019; Zander 1993).

Recent investigations have revealed the existence of a large number of new genera and even families of

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permineralized mosses and other bryophytes based on internal anatomy (Tomescu et al. 2018). However, most of the fossil bryophytes are represented by compression/impression fossils of obscure affinities from deposits that range from the Triassic (Bomfleur et al. 2014) to the Cretaceous (Cantrill 2000; Ignatov & Maslova 2021; Kudlecová 2020). In this paper we report on permineralized moss gametophytes with internal anatomy from the Santa Marta Formation of James Ross Island (James Ross Basin) off the northeastern coast of the Antarctic Peninsula. These Cretaceous mosses are most similar to taxa today included in Rhabdoweisiales D.Bell & Goffinet (Bechteler et al. 2023), or Dicranales s.l., Family: Rhabdoweisiaceae Limpr. (Fedosov 2021; Larraín 2020). Detailed anatomy of stems, leaves, rhizoids and the occurrence of probable pseudoparaphyllia and gemmae make this the most completely known moss gametophyte from Gondwana.

## METHODS

An anatomically preserved moss gametophyte with four major stem segments has been identified in a marine carbonate concretion collected by Peter Ward (University of Washington) from the Baculites Hill locality, near Scasso Peak (Nývlt & Šerák 2009), northern James Ross Island, Antarctica, 63°52′35″S, 57°54′00″W. Cretaceous strata exposed along Baculites Hill belong to the Beta Member of the Santa Marta Formation, which, based on magnetostratigraphy and biostratigraphy, is early to middle Campanian in age (ca. 80 Ma) (Milanese et al. 2019). Anatomical sections were prepared using the traditional cellulose acetate peel technique (Joy et al. 1956) with slabs etched in 5% HCl for ~15 seconds. Peels were mounted on microscope slides in Eukitt, a xylene soluble mounting medium (O. Kindler, Freiberg, Germany). Photographs were taken with a Better Light digital scanning camera (Better Light, Placerville, CA, U.S.A.) using transmitted lighted focused through a Leitz Aristophot large format camera with Summar lenses or a Zeiss WL compound microscope. Photographs were processed with Adobe Photoshop and **Figs. 3B** & **D** were focus stacked (Adobe, San Jose, CA, U.S.A.). Slides are reposited at the University of Washington, Burke Museum, Seattle, WA, U.S.A.

For comparative purposes we have used the review of fossil mosses of Ignatov & Maslova (2021) for interpreting fossil taxa. Bechteler et al. (2023) was used for the latest systematic treatment of extant mosses, as some of the families traditionally included within Dicranales have been reclassified in different families or even different orders.

## TAXONOMY

**Class**: Bryopsida McClatchie
**Subclass**: Dicranidae Doweld
**Order**: Rhabdoweisiales D.Bell & Goffinet
**Family**: Rhabdoweisiaceae Limpr.

**Jamesrossia** Z.Walker, Stockey, Rothwell, Atkinson, S.Y.Smith & Iglesias, *gen. nov*.

*Gametophyte three-dimensionally branched. Stem with central strand; numerous rhizoids at branch point. Phyllotaxis helical. Leaves costate, ensheathing, plicate. Leaf lamina unistratose. Leaf margins recurved, often bistratose. Costa simple, D-shaped in cross section, with 2–4 large guide cells. Laminar cells elongate.*

**Type species**: *Jamesrossia plicata* Z.Walker, Stockey, Rothwell, Atkinson, S.Y.Smith & Iglesias

**Jamesrossia plicata** Z.Walker, Stockey, Rothwell, Atkinson, S.Y.Smith & Iglesias, *sp. nov*.

Figs. 1–3

*Gametophyte loose cushion forming. Main shoot at least 210 μm in diameter; central strand at least 7 cells wide; cortex of thin-walled isodiametric cells, thicker walled toward stem margin; epidermis of small thicker walled rhomboidal cells. Branches at least 3.7 mm long and 90–100 μm wide. Rhizoids smooth, multicellular, occasionally branched, with oblique cross walls, 6–12 μm in diameter. Leaves dense, distinctly plicate, regularly spaced on branches, 650–700 μm wide, at least 700 μm long, overlapping. Costa percurrent, 90 μm wide and 55 μm thick. Laminar cells elongate, rectangular, L/W=5:1, quadrate in transverse section, lacking ornamentation. Gemmae rhizoidal, elongate, 61–78 μm long, 14 μm wide; multicellular (4–5 cells); cells with sinuous walls.*

TYPE: ANTARCTICA: Brandy Bay area of James Ross Island, Baculites Hill, 63°52′35″S, 57°54′00″W, (UWBM [University of Washington, Burke Museum] 116051 B bottom [slides 1–250], holotype).

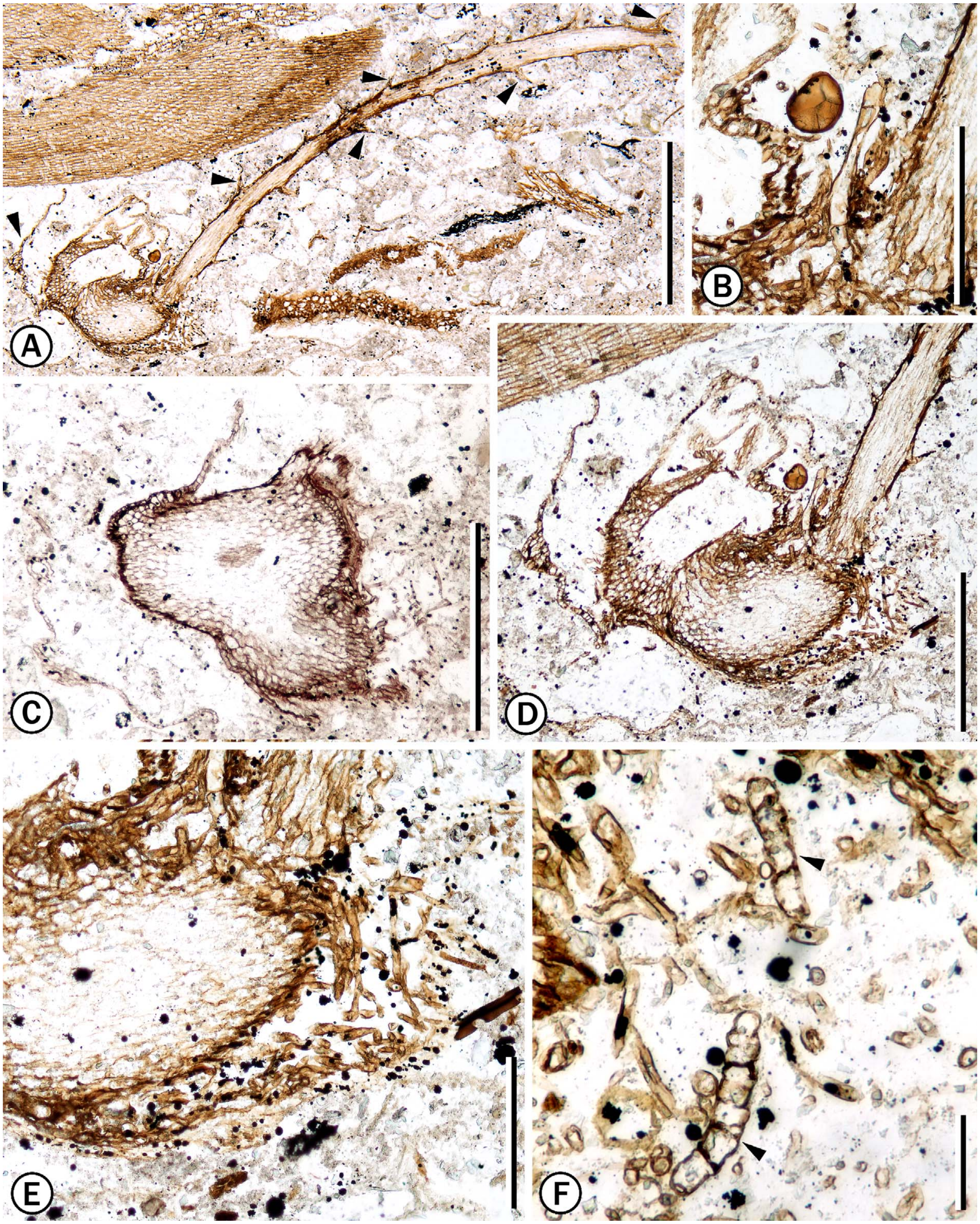

**Figure 1.** *Jamesrossia plicata* gen. et sp. nov., UWBM 116051. **A.** Transverse section of leafy gametophyte stem with attached branch in longitudinal section and rhizoids near bottom. Arrowheads indicate leaves. B bottom #93. Scale bar = 500 µm. **B.** Enlargement of junction of stem and branch (right) in **A**, showing trilete spore of probable vascular plant (center), stem leaf at left, possible pseudoparaphyllium (right) with large terminal cell and two smaller cells. B bottom #93. Scale bar = 100 µm. **C.** Stem in transverse section with central conducting strand and attached leaf upper left. B bottom #106. Scale bar = 30 µm. **D.** Transverse section of stem with attached leaves and rhizoids bottom right. B bottom #93. Scale bar = 20 µm. **E.** Stem with attached rhizoids near branch. B bottom # 93. Scale bar = 100 µm. **F.** Probable rhizoidal gemmae (at arrowheads). B bottom # 60. Scale bar = 33 µm.

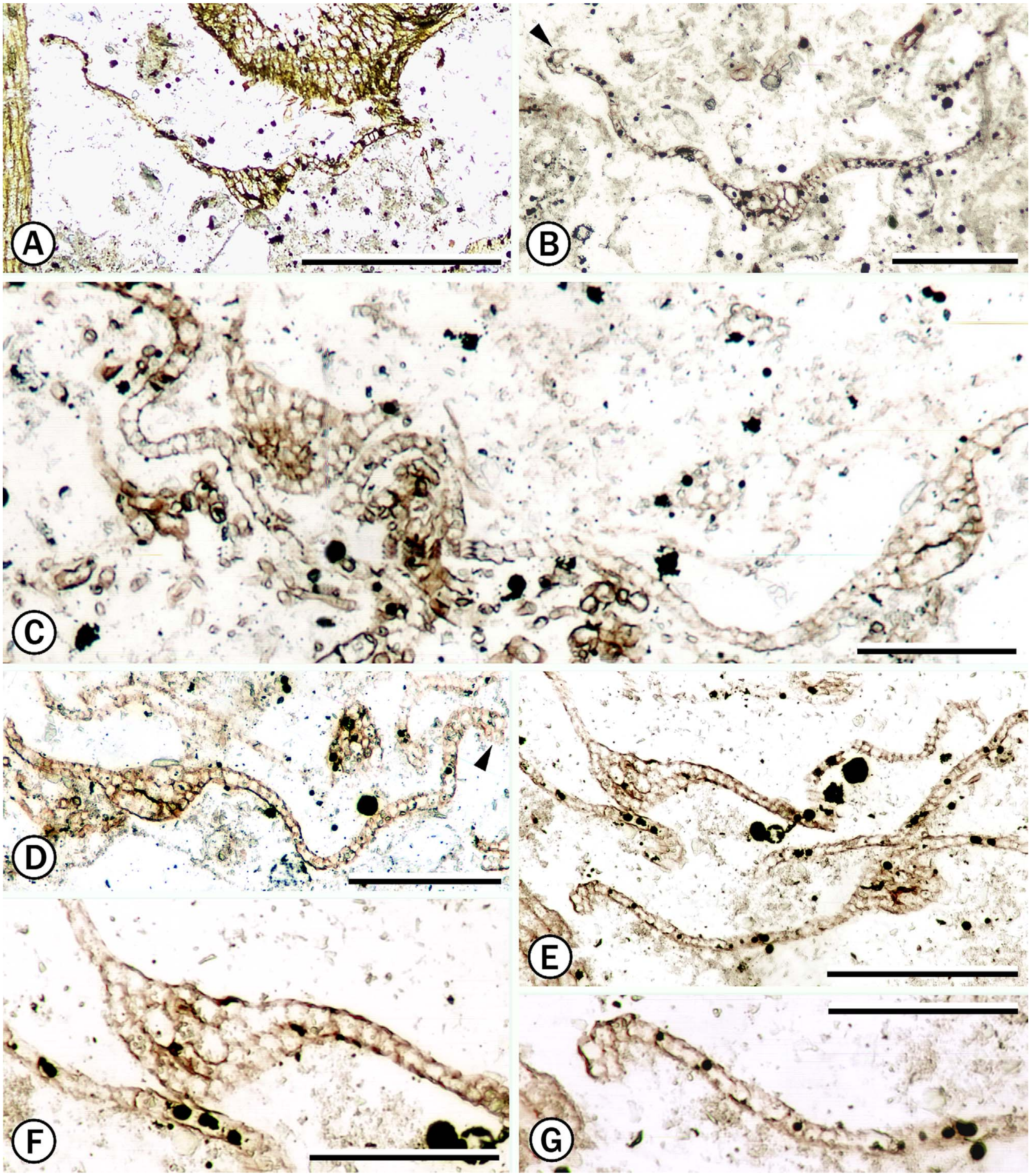

**Figure 2.** *Jamesrossia plicata* gen. et sp. nov. UWBM 116051. **A.** Transverse section of plicate leaf showing simple D-shaped costa. B bottom #93. Scale bar = 300 μm. **B.** Transverse section of plicate leaf with simple D-shaped costa showing one bi-stratose margin (arrowhead). B bottom #167. Scale bar = 100 μm. **C.** Several plicate leaves in transverse section at widest point with detailed costal anatomy and scattered rhizoids. B bottom #60. Scale bar = 50 μm. **D.** Transverse section of leaf showing unistratose lamina, pronounced plications and bistratose margin (arrowhead). B bottom #60. Scale bar = 100 μm. **E.** Several leaves in transverse section showing recurved bistratose margins. B bottom #56. Scale bar = 100 μm. **F.** Costal anatomy of leaf in transverse section. B bottom #56. Scale bar = 50 μm. **G.** Recurved bistratose leaf margin. B bottom #56. Scale bar = 50 μm.

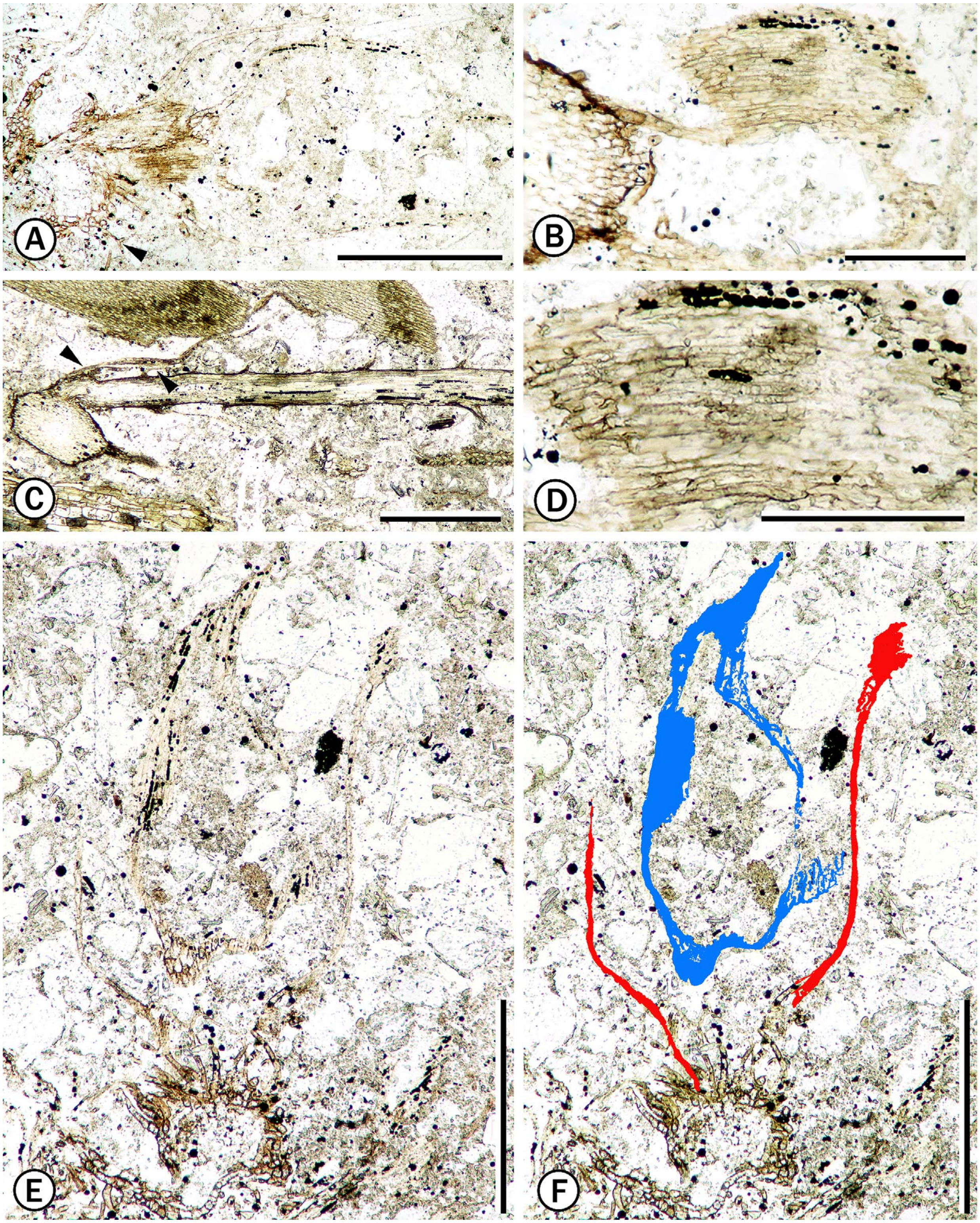

**Figure 3.** *Jamesrossia plicata* gen. et sp. nov. UWBM 116051. **A.** Stem in transverse section (left); leaf at right originating from lateral branch (out of plane of section). Note branching rhizoid (arrowhead). B bottom #53. Scale bar = 200 µm. **B.** Paradermal section of leaf near base. B bottom #141. Scale bar = 100 µm. **C.** Longitudinal section of branch (at right) showing overlapping leaves (arrowheads). B bottom #152. Scale bar = 200 µm. **D.** Paradermal section of leaf showing elongate cells near leaf base. B bottom #141. Scale bar = 100 µm. **E.** Leaf shown in A, near paradermal section showing general shape. B bottom #51. Scale bar = 200 µm. **F.** Leaf in E highlighted. Leaf margin (red), leaf center (blue), separated in drawing due to plication. B bottom #51. Scale bar = 200 µm.

***Stratigraphic position and age.*** Late Cretaceous (middle Campanian), Beta Member, Santa Marta Formation (ca. 80 Ma).

***Description.*** Four main stems of a three-dimensionally branched gametophyte appear to show a loose cushion forming habit with numerous rhizoids produced at branch points and helically arranged overlapping leaves on both the larger and smaller axes (**Fig. 1A**). The largest stem is at least 210 μm in diameter and has a central strand of thicker walled, small cells that is at least 7 cells wide. The cortex is composed of thin-walled cells that appear isodiametric in transverse section, that are thick-walled, and appear darker in color toward stem margin. The epidermal cells are thick-walled and rhomboidal, smaller than those of the cortex in cross section (**Fig. 1C**).

Three branches occur on one of the stems (**Fig. 1A, C**). Branches are at least 3.7 mm long and 90–100 μm wide and show large numbers of rhizoids at branch bases (**Fig. 1A, B**, **D, E**, **F**). Rhizoids are multicellular with oblique cross walls, smooth surfaces (**Fig. 1E, F**) and are 6–12 μm in diameter. Occasional branched rhizoids have been observed (**Fig. 3A**).

Leaves are closely spaced and helically arranged on branches (**Figs. 1A**, **3C**). Leaves appear to be decurrent and appressed to the stem (**Figs. 1A, C**), 650–700 μm wide, at least 700 μm long, imbricate and overlap one another (**Fig. 3C**). The costa is simple, D-shaped, percurrent, 90 μm wide and 55 μm thick, with 2 (–4) large guide cells (**Figs. 2A–F**). Small cells abaxial to the guide cells appear to represent substereids (**Figs. 2A–F**). The leaf lamina is unistratose and plicate, and cells are quadrate in transverse section, lacking any ornamentation (**Figs. 2A–G**). There are usually two plications on either side of the costa (**Figs. 2B–E**). Leaf margins are recurved and often bistratose (**Figs. 1C** at left bottom, **2A–2E**, **G**). Laminar cells are elongate and rectangular near base, L/W= 5:1 (**Figs. 3A, B**, **D, E**).

We examined serial sections of leaves in order to interpret over-all leaf structure. **Fig. 3F** outlines the leaf in **Fig. 3E**. Since leaves are very plicate, the blue section near the center of that leaf could be interpreted as the center of the leaf and the red section to be the margin of the same leaf (**Fig. 3F**; compare the paradermal leaf section in **Figs. 3E** and **F** with the transverse leaf section in **Fig. 2D**). However, in consecutive sections these appear to be two overlapping imbricate leaves. **Figs. 3E** and **F** show that leaves are slightly constricted at the base. Most of the leaves have been abraded prior to preservation, but they appear to narrow near the leaf tip. The costa continues to the tip (i.e., is percurrent), and there is no evidence of a protruding awn or excurrent costa in the most complete leaves.

One linear structure 18 μm in diameter that includes a large apical cell and two smaller basal cells has been identified at one of the branching points of the gametophyte (**Fig. 1B**). There is a distinct size difference between the cells of this structure and those of rhizoids that typically measure 6–12 μm in diameter. This structure compares favorably with filamentous pseudoparaphyllia (e.g., Akiyama 1990a,b) produced by some extant mosses (see discussion below).

Two distinct, elongate multicellular structures four to five cells long occur among the rhizoids (**Fig. 1F**). We interpret these as filamentous rhizoidal gemmae. Cell walls of these structures appear sinuous and thicker walled than typical rhizoids (**Fig. 1F**). Cells of the gemmae are 61–78 μm long and 14 μm wide.

A single large trilete spore 56 μm in diameter apparently was trapped between two leaves near a branch point (**Fig. 1B**). This spore lacks any visible ornamentation and its large size suggests that it represents a vascular plant, perhaps a fern and has nothing to do with the moss per se.

***Etymology.*** The genus is named for occurrence on James Ross Island. The specific epithet refers to the distinctly plicate leaves of this moss.

## DISCUSSION

*Jamesrossia plicata* has branched stems with a central strand. Leaves are numerous and helically arranged around the stem, plicate, and long-lanceolate; with a single, strong, D-shaped costa. The costa is percurrent and smooth on the abaxial surface. Laminal cells are smooth, with non-pitted walls and proximal cells that are elongate, apparently undifferentiated in the alar region; and have numerous rhizoids near branch origins and leaf bases. This combination of characters fits well within the family Dicranaceae s.l. (Ireland 2007). Recent phylogenomic studies have substantially revised relationships within Dicranales s.l. and several traditionally understood families are now considered orders. Within Dicranidae and Dicranales s.l., the Antarctic moss shows the closest similarities to taxa in the Rhabdoweisiales (Bechteler et al. 2023), Rhabdoweisiaceae (sensu Larraín et al. 2020), some of which still occur in Antarctica today (Ochyra et al. 2008). Among the 11 genera included in the family Rhabdoweisiaceae, leaf anatomy of the new fossil Antarctic moss most closely compares to species of *Arctoa* Bruch & Schimp., *Cynodontium* Bruch & Schimp., *Dicranoweisia* Lindb. ex Milde, *Oncophorus* Brid., and *Oreas* Brid.

The small genus *Arctoa* from Asia, Europe and North America consists of four species that usually have a wider costa than *Jamesrossia* and leaves that lack recurved margins ending in a multistratose acuminate tip (Ireland 2007; Lüth 2019; Noguchi 1987). *Arctoa hyperborea* (Gunnerus ex Dicks.) Bruch & Schimp shows the closest similarity to *Jamesrossia plicata* in costal anatomy with two median guide cells and poorly developed stereids (Chien et al. 1999; Lüth 2019). However, the leaves of *A. hyperborea* have a distinct subulate apex (Chien et al. 1999, Lüth 2019) that is lacking in *J. plicata*. In addition, median guide cells on the adaxial side of the leaf appear to be continuous with the lamina in transverse section in *A. hyperborea* near the leaf tip (Chien et al. 1999; Lüth 2019); while leaves of *Jamesrossia* have two median guide cells that do not come in contact with the adaxial leaf surface in any sections that we have observed. In *Jamesrossia* cells in the alar region are rectangular and not noticeably differentiated, while in *A. hyperborea* cells are distinct, quadrate and slightly enlarged (Chien et al. 1999; Ireland 2007; Lüth 2019).

*Oncophorus* with six species from North America, Europe and Asia, like *Arctoa,* contains taxa that display a wider costa (Ireland, 2007; Lüth 2019; Noguchi 1987) than our fossil. There are two stereid bands that are very pronounced in leaf transverse section in most species of *Oncophorus* (Lüth 2019), which are lacking in *Jamesrossia*. *Oncophorus integerrimus* Hedenäs is the most similar to *J. plicata* with recurved, bistratose margins and what appears to be two median guide cells in distal leaf sections (Lüth 2019). Guide cells increase in number toward the leaf base in *O. integerrimus*, and the costa is thicker showing the typical stereid bands seen throughout the leaf in other *Oncophorous* species (Lüth 2019). In *J. plicata* stereids cells are poorly developed, and we consistently see two median guide cells unlike those in most *Oncophorus* species.

The genus *Cynodontium* consists of 15 species native to temperate and arctic regions of the Northern Hemisphere (Ireland 2007). Within *Cynodontium,* some species have recurved, bistratose margins and poorly developed stereid bands (Ireland 2007). Most *Cynodontium* species show leaves that are mamillose on both surfaces (Lüth 2019; Noguchi 1987) while those of *Jamesrossia* generally have smooth surfaces. The most similar species within this group appears to be *C. tenellum* (Schimp.) Limpr., which generally lacks the mamillose surface of other *Cynodontium* species (Ireland 2007; Lüth 2019). However, leaves of *C. tenellum* lack the plications present in *Jamesrossia,* have a slightly stouter costa near the base (Lüth 2019), and have occasional distal papillae (Ireland 2007).

*Oreas* is a monotypic genus found in North America, Europe and Asia (Ireland 2007). Leaves of *Oreas martiana* (Hoppe & Hornsch.) Brid. are very similar to those of *Jamesrossia* in transverse section with a D-shaped costa, two central guide cells, poorly developed stereids, unistratose laminae with recurved bistratose margins, and smooth surfaces (Kiebacher & Roloff 2020; Lüth 2019). Cells in the alar region of *O. martiana*, however, are rectangular and not differentiated (Ireland 2007; Kiebacher & Roloff 2020; Lüth 2019), compared to the more elongate cells seen in *Jamesrossia,* and their lateral laminae lack distinct plications.

*Dicranoweisia* with about 20 widespread species occurs in both North and South America, Europe, Asia, Africa, Pacific Islands, Hawaii, New Zealand, Australia and Antarctica (Ireland 2007). Some of the species have a stout costa e.g., *D. crispula* (Hedw.) Mild., and unistratose laminae (Noguchi 1987). Leaves of *Jamesrossia* are most similar to those of *D. cirrata* (Hedw.) Lindb. ex Milde, which are unistratose with smooth surfaces, unistratose and bistratose margins, poorly developed stereids and two median guide cells (Lüth 2019). Cells of the leaf lamina are similar to those of *Jamesrossia* in shape both in the alar region and nearer the leaf tip. In addition, *D. cirrata* produces multicellular gemmae on leaf abaxial surfaces (Ireland 2007). These are short (with 4–10 cells), linear, smooth, with occasional biseriate portions (Ireland 2007). Such gemmae are very similar to the two structures that we interpret as gemmae on the abaxial surface of leaves in *Jamesrossia*. Leaves of *D. cirrata* are generally narrower than those of *Jamesrossia*, and leaves in the extant species lack plications (Lüth 2019).

***Paraphyllia vs. pseudoparaphyllia.*** One elongate linear structure consisting of two small basal cells and one large, elongate, apical cell is interpreted as a filamentous pseudoparaphyllium (see **Fig. 1B**). These cells are larger in diameter than those of rhizoids and their position at a branching point make this structure distinctly different from any leaf cells. Such structures have been termed paraphyllia or pseudoparaphyllia in extant mosses (Akiyama 1990a,b; Akiyama & Nishimura 1993; Ireland 1971; Spirina et al. 2020). There are two morphologies of such structures; some are leafy, while others are linear, filamentous, multicellular and may be branched (Spirina et al. 2020). Their placement in different moss species may make them taxonomically significant for some mosses (Ireland 1971), but they need to be studied in detail. It is important to distinguish these structures from rhizoids, "mucilage hairs," micronemata, or paraphyses (Ignatov et al. 2022; Ireland 1971; Spirina et al. 2020). While pseudoparaphyllia are defined in relation to branch primordia, they also still can be identified when branches are mature, but singularly and not usually in clusters. The structure seen in *Jamesrossia* is filamentous, uniseriate, and associated with a mature branch. Paraphyllia, on the other hand, is a term usually used for adventitious structures of the stem epidermis as used by Akiyama and Nishimura (Akiyama 1990a,b, Akiyama & Nishimura 1993; Spirina et al. 2020). While there seems to be some disagreement about the use of the terms and the development of these structures, Ireland (1971) suggested that a more thorough study in mosses would prove useful taxonomically.

***Comparison to fossil mosses.*** Studies of fossil bryophytes have increased dramatically in recent years. However, many of the described fossil taxa are compressions without internal anatomy and it is often very difficult to determine whether some specimens are actually mosses at all (Ignatov & Maslova 2021). Bippus et al. (2022) reviewed the types of fossil bryophyte preservation and the types of information that they reveal. Permineralization, such as in the fossils described here, produces fossils with the most information on anatomy and morphology (Bippus et al. 2022). Recently, Ignatov & Maslova (2021) critically reviewed the fossil record of mosses, and we use their analyses to focus our discussion to the relevant permineralized and/or Antarctic taxa and those accepted in Dicranidae by these authors.

*Merceria angustica* Smoot & Taylor (1986) is an anatomically preserved moss described from the silicified peats at Skaar Ridge, in the Permian Transantarctic Mountains of Antarctica. Some stem specimens contained a few thick-walled cells of a conducting strand. Costae are up to six cells thick and rather homogeneous (Ignatov & Maslova 2021). The lamina is consistently unistratose (Smoot & Taylor 1986). The costa of *M. angustica* is large and sometimes up to one half of the width of the leaf (Smoot & Taylor 1986), while the costa in *Jamesrossia* is narrow and occupies less than one third of the leaf base. In addition, *Jamesrossia* has two prominent guide cells which are lacking in *M. angustica*.

Fossil mosses have been reported previously from the Cretaceous of James Ross Island and nearby Snow Island (Cantrill 2000; Kadlecová 2020) as *Muscites* Brongn., a name used for putative fossil mosses (usually compression fossils) whose affinities are unknown. Some specimens show much more anatomical detail than others, e.g., *Muscites* sp. 1-3 Kadlecová (2020) from the Cretaceous of James Ross Island and also the Czech Republic. *Muscites* sp. 1 (Kadlecová 2020) comes from the Hidden Lake Formation (Coniacian) of James Ross Island and is represented by compressions that show leaves that are not overlapping at the base, with a stout percurrent costa. Anatomical details are lacking but the overall leaf morphology differs considerably from the overlapping plicate leaves of *Jamesrossia*. *Muscites* sp. 3 (Kadlecová 2020) also comes from James Ross Island, slightly younger Santa Marta Formation, but transverse sections of the costa are lacking, and it is difficult to determine any affinities due to the lack of anatomical detail. The small leaves with a stout costa have lead Ignatov and Maslova (2021) to suggest affinities with the distantly related Mniaceae within Bryales.

*Livingstonites gabrielae* Vera from the Cerro Negro Formation, Early Cretaceous (Aptian) of Livingston Island, South Shetland Islands, Antarctica (Vera 2011) appears to be permineralized, and was studied using thin sections. The stem has a central conducting strand (Vera 2011) as does *Jamesrossia*. Leaves of *L. gabrielae* are narrowly linear to subulate with elongate laminar cells (Vera 2011). The costa has large guide cells and appears to have a band of abaxial stereids. The sections illustrated do not allow for a detailed view of all costal cells in cross section, and this species needs to be reexamined, perhaps using cellulose acetate peels. Nonetheless, *L. gabrielae* shows similarities to Dicranaceae based on leaf characters (Ignatov and Maslova 2021). The leaves are narrower than those of *Jamesrossia plicata*, subulate, and do not seem to be plicate. In addition, the costa is larger over-all and contains greater numbers of cells and seems to have a larger stereid band. Similar leaves described as *Livingstonites* sp. 1 have been found in the Czech Republic (Kadlecová 2020). *Livingstonites* sp. 1 also comes from James Ross Island and the Santa Marta Formation (Kadlecová 2020). A detailed view of the costal anatomy would provide more diagnostic characters for taxon placement. Ignatov and Maslova (2021) have listed the taxonomic placement of these fossils in *Livingstonites* as highly doubtful.

*Campylopodium allonense* Konopka, Herendeen & Crane from the Late Cretaceous (Santonian) of Georgia, U.S.A. (Dicranaceae) was described from carbonaceous clay lenses in the Allon Quarry (Konopka et al. 1998). The material is well preserved and includes both sporophytes and associated gametophytes. The gametophytes have leaf tips that are slightly abraded but show unistratose margins and the margins are recurved as in *Jamesrossia*. However, no evidence of a bistratose margin has been found in the associated Allon gametophytes. In *C. allonense* the costa shows three to five guide cells (Konopka et al. 1998) rather than the typically two distinct guide cells seen in *Jamesrossia*. In *C. allonense* there are distinct abaxial and adaxial stereid bands that are lacking in *Jamesrossia*.

An Eocene moss gametophyte preserved in the Baltic Amber described as *Cynodontium eocenicum* Ignatov & Jan Kučera was placed in the extant genus (Ignatov et al. 2016). The linear lanceolate, strongly channeled leaves with subpercurrent costa, serrulate leaf apices, and papillose cells prompted these authors to place the moss in *Cynodontium* (Ignatov et al. 2016). Unlike this Eocene moss, *Jamesrossia* lacks channeled leaves and papillose cells.

*Cynodontium luthii* Bippus, Rothwell & Stockey (2021) was described from a permineralized gametophyte from a Late Cretaceous locality along the Colville River in northern Alaska. Bippus et al. (2021) included this taxon in the Rhabdoweisiaceae based on its similarities to extant *Cynodontium*. Like *Jamesrossia*, *C. luthii* has a central conducting strand and sheathing leaves that are reported to have a unistratose lamina, occasional bistratose margins, D-shaped costa with similar costal anatomy, including an upper and lower epidermis, small number of abaxial stereids and few guide cells (Bippus et al. 2021). However, the leaves of *C. luthii* extend to a pronounced excurrent costa that shows a distinct channel in transverse section (Bippus et al. 2021). We see no evidence for strongly channeled leaves in *Jamesrossia*. Furthermore, leaves of *C. luthii* lack distinct plications or pronounced recurving of the leaf margins as occur in *Jamesrossia*. In addition, rhizoids are borne on the channeled portions of the adaxial surfaces of leaves in *C. luthii* (Bippus et al. 2021), while in *Jamesrossia* they occur associated with branches.

## CONCLUSIONS

While *Jamesrossia plicata* is most similar in morphology and anatomy to extant *Oreas* and *Dicranoweisia*, leaves show several minor differences. It seems evident that this fossil taxon should be included in Rhabdoweisiales, Family: Rhabdoweisiaceae Limpr. sensu Larraín (2020), a group today segregated from the Dicranales s.l. (Bechteler et al. 2023). Without sporophytes, color, and more information on growth habit we do not feel confident in assigning it to an extant genus. These fossil gametophytes had a conducting strand and slightly thickened cells near the stem margin. Rhizoids are concentrated near the base of branches along with small multicellular, linear gemmae. The most important preserved taxonomic characters, however, appear to be in the leaves, with sheathing bases, smooth laminal cells, a small D-shaped costa in cross section, recurved margins that are unistratose or bistratose, quadrate cells in cross section, with rectangular cells in the alar region that fit well into this group of mosses.

The description of this new fossil moss as *Jamesrossia plicata* adds another Upper Cretaceous occurrence of the Rhabdoweisiaceae, which is roughly concordant with the clade age estimations of Bechteler et al. (2023). Both *Cynodontium luthii* (Bippus et al. 2021; Campanian – Maastricthian of Alaska) and *J. plicata* (Campanian of Antartctica) are essentially coeval suggesting that at their earliest appearance, Rhabdoweisiaceae were geographically widespread in near polar regions in both boreal and austral realms.

Moreover, at their earliest appearance, during the Campanian, they are found in northern and southern (sub) polar regions.

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