



FOSSIL MOSSES FROM THE EARLY CRETACEOUS CATEFICA MESOFOSSIL FLORA, PORTUGAL – A WINDOW INTO THE MESOZOIC HISTORY OF BRYOPHYTES

BENJAMIN BOMFLEUR^{1,*}, LARS HEDENÄS², ELSE MARIE FRIIS^{3,4}, PETER R. CRANE^{5,6}, KAJ RAUNSGAARD PEDERSEN³, MÁRIO MIGUEL MENDES^{7,8}, JIŘÍ KVAČEK⁹

¹Institute of Geology and Palaeontology, Palaeobotany, University of Münster, Heisenbergstr. 2, D-48149 Münster, Germany; e-mail: bbomfleur@uni-muenster.de.

²Department of Botany, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden; e-mail: lars.hedenas@nrm.se.

³Department of Geoscience, University of Aarhus, Høegh-Guldbergs Gade 2, DK-8000 Aarhus C Denmark.

⁴Department of Palaeobiology, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden.

⁵Oak Spring Garden Foundation, 1776 Loughborough Lane, Upperville, Virginia 20184 USA.

⁶Yale School of Environment, Yale University, New Haven, Connecticut 06511 USA.

⁷University of Coimbra, MARE – Marine and Environmental Sciences Centre/ARNET – Aquatic Research Network, Earth Sciences Department, Rua Sílvio Lima, Pólo II, 3030-790 Coimbra, Portugal.

⁸Fernando Pessoa University, Praça 9 de Abril 349, Porto 4249-004, Portugal.

⁹National Museum Prague, Václavské nám. 68, 115 79 Praha 1, Czech Republic.

*corresponding author

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Abstract: A diverse assemblage of mosses from the Early Cretaceous Catefica mesofossil flora, Portugal, is described based on fragments of charcoaled and lignitized gametophytes and a single spore capsule. Nine different gametophyte morphologies are recognized and assigned to Sphagnopsida, Polytrichopsida and Bryopsida. None of the fossils can be included in any extant species. Four species have character combinations not known in any extant genera and are accommodated in three new genera as *Chlorosphagnum cateficense* gen. et sp. nov. (Sphagnales, family *incertae sedis*), *Physcidium tortuosum* gen. et sp. nov. and *Physcidium simsimiae* sp. nov. (Diphysciales, Diphysciaceae), and *Canaliculidium fissuratum* gen. et sp. nov. (Dicranales, Leucobryaceae). Three other species can be assigned to extant genera and are described here as *Polytrichastrum incurvum* sp. nov. (Polytrichales, Polytrichaceae), *Dicranodontium minutum* sp. nov. and *Campylopus lusitanicus* sp. nov. (both Dicranales, Leucobryaceae). One additional specimen has features suggesting affinity with Leucobryaceae but lacks characters critical for a definite generic placement. A single spore capsule is unassigned but is similar to capsules of members of the Ditrichaceae (Dicranales). All the fossil mosses recognised in the Catefica mesofossil flora are assigned to orders of extant mosses that diverged prior to the diversification of the Bryidae, the most diverse clade of living mosses. Based on extrapolations from their nearest living relatives, the Catefica mosses likely grew in more or less open environments, and in moist or wet sites that were primarily of low pH and low nutrient status.

Key words: Almage formation, Bryophyta, Early Cretaceous, fossil mosses, mesofossils, SRXTM, synchrotron radiation X-ray tomographic microscopy

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Introduction

Lagerstätten of charcoaled mesofossils have long been recognized as an extraordinary source of new information on fossil plant anatomy, systematics and phylogeny (Harris 1958, 1981, Alvin 1974, Scott 1974, Friis and Skarby 1981, Friis 1984, Edwards et al. 1992, Friis et al. 2006, 2007, Edwards and Richardson 2004, Eklund et al. 2004, Glasspool et al. 2006). This is especially true of Cretaceous-

age accumulations of charcoaled and lignitized fossils, which over the last few decades have yielded unprecedented insights into early angiosperm evolution (Friis 1983, Herendeen et al. 1999, Friis et al. 2006, 2019a, 2022), as well as the diversity among contemporary gymnosperms (Friis et al. 2007, 2009, 2019b). By comparison, cryptogams have received little attention in studies of Cretaceous charcoaled and lignitized mesofossil assemblages, even though they can

be exquisitely well-preserved, as illustrated by the detailed information obtained from fossils of small gleicheniaceus ferns (Gandolfo et al. 1997, see also Herendeen and Skog 1998), as well as gametophytes and sporophytes of mosses from the Cretaceous of North America (Konopka et al. 1997, 1998).

The sparse documentation of bryophytes in the fossil record, in comparison with vascular cryptogams and seed plants, has led to the conclusion that the fossil record of these plants is especially incomplete due to their small size, delicate nature, and presumed overall low fossilization potential (see, e.g., Oostendorp 1987, Tomescu et al. 2018, Ignatov and Maslova 2021). However, given suitable taphonomic conditions, bryophytes can be preserved with great completeness and structural fidelity (Tomescu et al. 2018, Bippus et al. 2022).

Here we report the discovery of an assemblage of mosses from the Catefica mesofossil flora of Portugal, which is of Early Cretaceous (Aptian–early Albian) age. Apart from a single capsule, the fossils are all exquisitely well-preserved three-dimensional gametophyte shoots. They are assigned to seven species in six genera. The seven species are distributed among four orders of extant mosses representing three classes – Sphagnales (Sphagnopsida), Polytrichales (Polytrichopsida) as well as Diphysciales and Dicranales (Bryopsida) – and comprise extinct taxa with character combinations unknown in the modern biota alongside forms that are almost indistinguishable from extant species.

Material and methods

The specimens come from the Catefica mesofossil flora extracted from sediment sample Catefica 49. The sample was collected by EMF, KRP and PRC in 1989 from sedimentary deposits of the Almargem Formation exposed in a road cut along Rua General Humberto Delgado, between the villages of Catefica and Mugideira, approximately 4 km south of Torres Vedras, Lusitanian Basin, western Portugal (39° 03' 30" N, 09° 14' 30" W). The sedimentary rocks are predominantly cross-bedded sands with subordinate horizons of clay and silt and contain abundant plant fragments preserved as three-dimensional charcoalfied or lignitized fossils that are slightly compressed. The precise position of the Catefica plant-bearing horizons in the Almargem Formation is uncertain, but they are either in the upper part of the Lower Almargem Formation or in the basal part of the Upper Almargem Formation, indicating a late Aptian–early Albian, or perhaps slightly older, age (Rey 1992, 1993, Dinis et al. 2008, 2010). For illustrations of the Catefica locality, further discussion of the age of the Catefica mesofossil flora, and the methods used to extract the mesofossils, see Friis et al. 2011, 2018, 2022. Other plant fossils from the Catefica mesofossil flora have been described by Friis et al. 2011, 2018, 2019a, 2022, Mendes et al. 2017, 2018a, Kvaček and Mendes 2020, 2021, Mendes and Kvaček 2020, and Tekleva et al. 2021.

The organic residues processed from sediment samples were sorted under a stereomicroscope to identify specimens for further study. Specimens for scanning electron microscopy (SEM) and synchrotron radiation X-ray tomographic microscopy (SRXTM) were mounted on metal stubs using nail polish. For SEM, specimens were sputter-coated with gold and examined using a Hitachi S-4300 field emission SEM and a Phillips 515 SEM at the Swedish Museum of Natural History, Stockholm. For SRXTM, twenty-four specimens were left uncoated and analyzed at the TOMCAT beamline of the Swiss Light Source of the Paul Scherrer Institute, Villigen, Switzerland (Stampanoni et al. 2006, Friis et al. 2014a). SRXTM measurements were done with projection over 180° using a sCMOS detector and a 20 µm thick LuAg:Ce scintillator screen at 10 keV, either with a x10 objective with isotropic pixel size of 0.65 µm (S156534, S156535, S266374–S266379, S266383–S266392) or with a x20 objective with isotropic pixel size of 0.325 µm (S171522, S174251, S266084, S266380–S266382). Most specimens were also vertically stacked. Reconstructions of SRXTM data were made using Avizo software and an even black background for the SEM images was generated using Adobe Photoshop.

Specimens described in this paper are housed in the palaeobotanical collections of the Swedish Museum of Natural History, Stockholm (S numbers). The names of the new taxa are registered with a unique number in the Plant Fossil Names Registry (PFNR) hosted and operated by the National Museum, Prague, Czech Republic, for the International Organisation of Palaeobotany (IOP). Datasets from SRXTM analyses are available at the PSI Public Data Repository, Paul Scherrer Institute, Villigen, Switzerland (Bomfleur et al. 2023).

Systematic palaeobotany

Division Bryophyta A. BRAUN, 1864

Class Sphagnopsida SCHIMP., 1857

Order Sphagnales LIMPR., 1885

Family *Incertae sedis*

**Genus *Chlorosphagnum* HEDENÄS, BOMFLEUR
et E.M.FRIIS gen. nov.**

Type species. *Chlorosphagnum cateficense* HEDENÄS, BOMFLEUR et E.M.FRIIS

Plant Fossil Names Registry Number. PFN003143.

E t y m o l o g y. Referring to the large chlorophyll cells in the leaves.

G e n e r i c d i a g n o s i s. A member of the Sphagnales with unusually large chlorophyll cells, approximately the same size as the hyaline cells in transverse section.

D i s t i n g u i s h i n g f e a t u r e s. *Chlorosphagnum* differs from all four extant genera of Sphagnales in having

proportionately larger chlorophyll cells. The chlorophyll cells are about the same size as the hyaline cells.

***Chlorosphagnum cateficense* HEDENÄS, BOMFLEUR
et E.M.FRIIS sp. nov.**
Text-figs 1a–g, 2a–d

Holotype. S156535 (Catefica sample 49; figured Text-fig. 1a, f).

Plant Fossil Names Registry Number. PFN003144.

Paratypes. S107796, S156534, S266377, S266380, S266381 [Catefica sample 49; figured Text-fig. 1b, c, e, g (S156534); Text-fig. 1d (S107796); Text-fig. 2a–d (S266380)]

Repository. Palaeobotanical Collections, Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden.

Etymology. Referring to the locality, Catefica, where the fossils were collected.

Type locality. Catefica (39° 03' 30" N, 09°14' 30" W), between the villages of Catefica and Mugideira, about 4 km south of Torres Vedras, Portugal.

Type stratum and age. Almargem Formation, Early Cretaceous (late Aptian–early Albian).

Specific diagnosis. Hyaline cells distinctly fibrillose.

Distinguishing features. This is the only species of *Chlorosphagnum* described thus far.

Description and Comments on the Material. The six specimens attributed to this species (S107796, S156534, S156535, S266377, S266380, and S266381) are portions of shoots 1.0–2.3 mm long with attached leaves. Leaves are ovate, gradually narrowed above into a broadly acuminate apex, and are 0.45–0.70 mm long (Text-figs 1a, b, 2a, b). Leaves are composed of two kinds of cells of similar size, i.e., between 5–10 µm wide when seen in transverse section (Text-figs 1d, e, 2c). Chlorophyll cells are large but are enclosed by hyaline cells (Text-figs 1d–g, 2c, d). The hyaline cells are distinctly fibrillose (Text-figs 1g, 2a, d). In the SEM images the hyaline cells look as if they consist only of rows of pores (e.g., Text-fig. 1a), but SEM images of *Sphagnum* L. in modern peat have a similar appearance (Rezanezhad et al. 2016) and we interpret these numerous 'pores' as a feature created by collapse of the cell walls between the fibrils. It could be argued that the diagnostically relevant similar size of chlorophyllose and hyaline cells could be a taphonomic artefact resulting from differential shrinkage during charcoalification; if that were so, however, it would be the living chlorophyllose cells that would be expected to show greater shrinkage than the empty hyaline cells, whose walls are reinforced with fibrils precisely to prevent cell shrinking and collapse.

Systematic Relationships. Sphagnales comprises only one family, Sphagnaceae Dumort., with four extant genera, *Ambuchanania* SEPPELT et H.A. CRUM ex A.J. SHAW, *Eosphagnum* A.J. SHAW, *Flatbergium* A.J. SHAW, and *Sphagnum* L. *sensu stricto*. *Chlorosphagnum cateficense* has chlorophyll cells in the leaves that are enclosed by hyaline cells, as is typical of all four extant genera. SEM images and images of longitudinal sections (Text-figs 1a, g, 2a, b, d) also show the distinct fibrils that are almost invariably present in hyaline cells of modern *Sphagnum* (Shaw et al. 2003). However, *C. cateficense* differs from all four extant genera in having chlorophyll cells that are approximately the same size as the hyaline cells. In extant species, when seen in transverse section, the chlorophyll cells are noticeably (and mostly much) smaller than the hyaline cells.

In overall leaf characters, including leaf-cell arrangement and also in the absence of a costa, *Chlorosphagnum cateficense* is clearly more similar to other fossil and extant members of *Sphagnum* (see Reissinger 1950, Frahm 2009) than to the Paleozoic Protosphagnales in which mature leaves have a costa and mostly a marginal border, and where all cells lack fibrils (e.g., Neuburg 1960, Oostendorp 1987, Ignatov 1990, Maslova and Ignatov 2013, Ignatov and Maslova 2021). The ontogeny of the leaf cells has also been suggested to differ in Sphagnales and Protosphagnales (Ivanov et al. 2018).

Class Polytrichopsida DOWELD, 2001
Order Polytrichales M.FLEISCH., 1920
Family Polytrichaceae SCHWÄGR., 1830
Genus Polytrichastrum G.L.SM., 1971

***Polytrichastrum incurvum* HEDENÄS, BOMFLEUR
et E.M.FRIIS sp. nov.**
Text-figs 3a–g, 4a–d

Holotype. S174251 (Catefica sample 49; figured Text-fig. 3a–g).

Plant Fossil Names Registry Number. PFN003145.

Paratypes. S266391, S266392 [Catefica sample 49; figured Text-fig. 4a–d (S266392)]

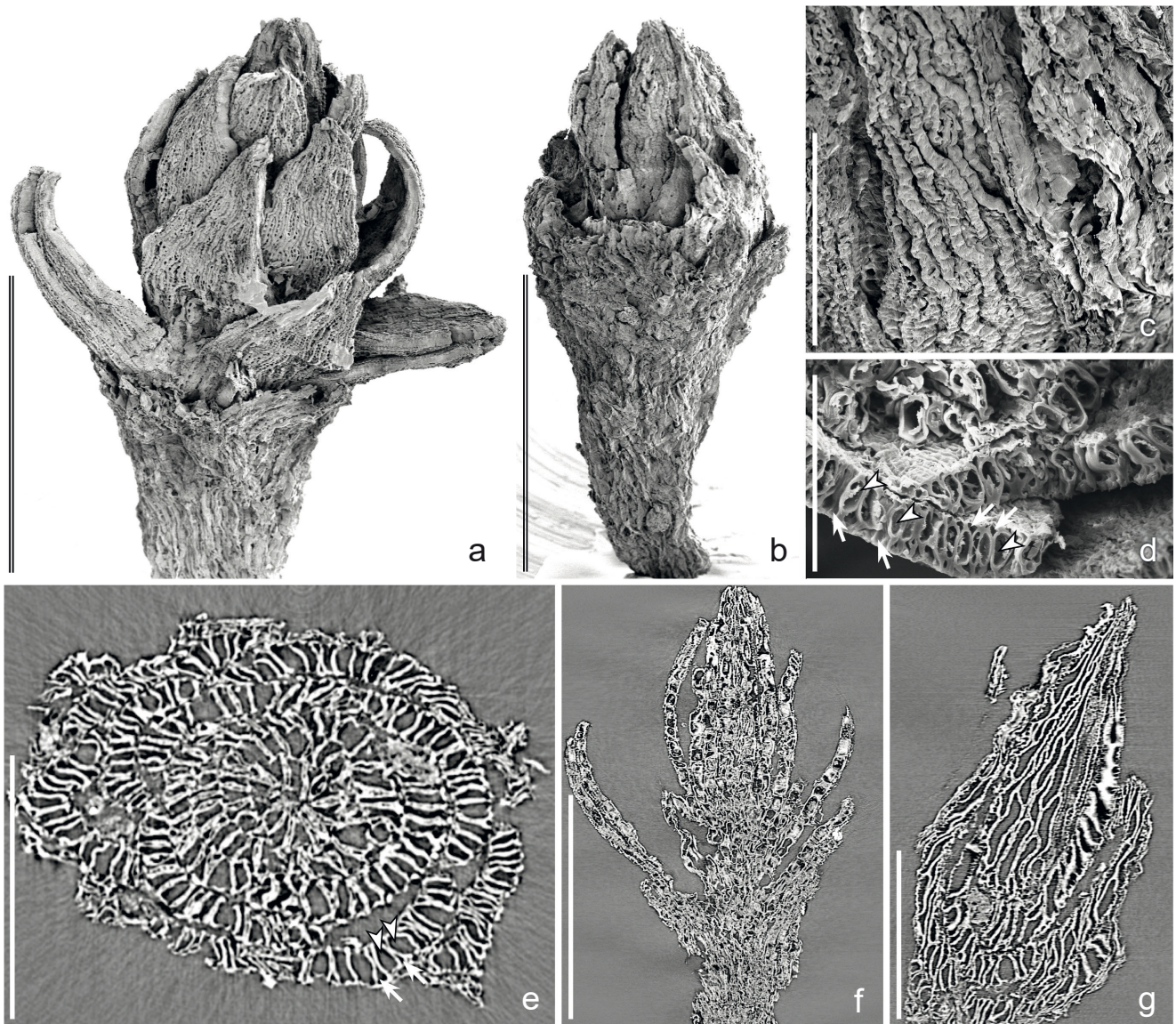
Repository. Palaeobotanical Collections, Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden.

Etymology. The specific epithet refers to the incurved leaf margins.

Type locality. Catefica (39° 03' 30" N, 09°14' 30" W), between the villages of Catefica and Mugideira, about 4 km south of Torres Vedras, Portugal.

Type stratum and age. Almargem Formation, Early Cretaceous (Aptian–early Albian).

Specific diagnosis. A species of *Polytrichastrum* G.L.SM. with distinctly incurved margins of the leaf limb



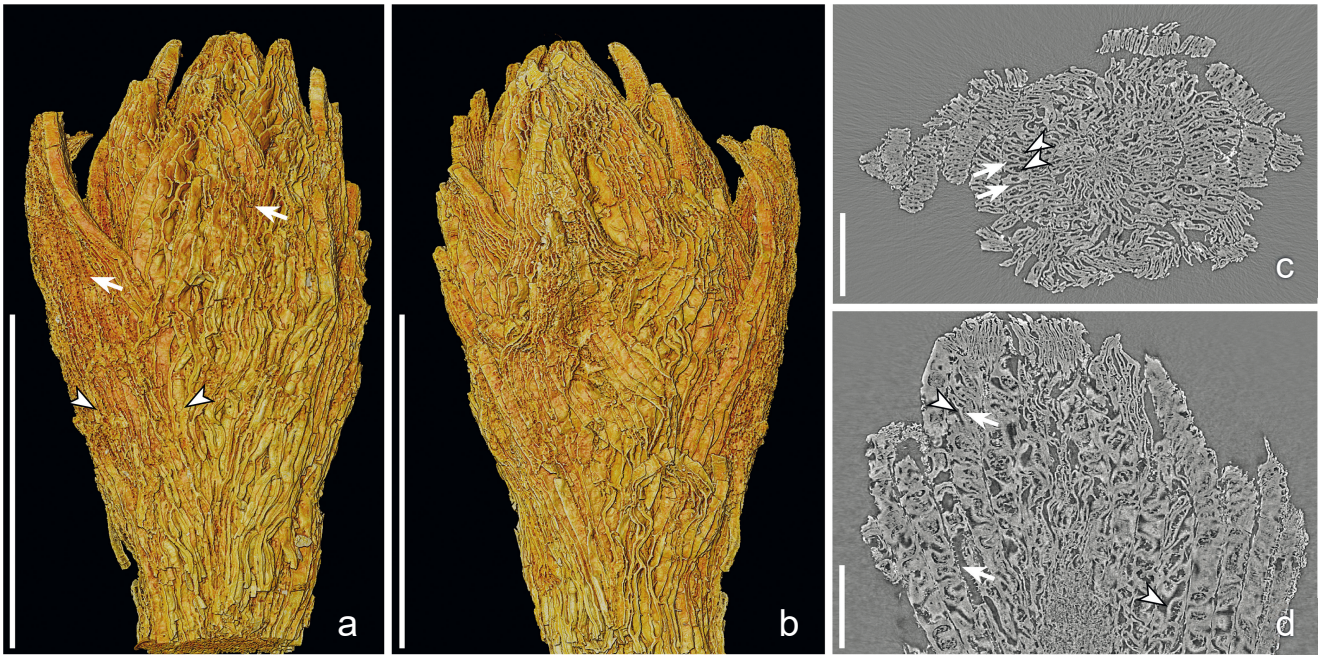
Text-fig. 1. Scanning electron microscope (SEM, a–d) and synchrotron radiation X-ray tomographic microscopy (SRXTM, e–g) images of shoots and leaves of *Chlorosphagnum cateficense* HEDENÄS, BOMFLEUR et E.M.FRIIS from the Early Cretaceous Catefica mesofossil flora, Almargem Formation, Portugal. a, b: Shoot apices with leaves showing rows of collapsed cell walls between the transverse fibrils of the hyaline cells. c: Detail of leaf surface showing cell pattern with many hyaline cells collapsed. d: Transverse sections of leaves showing differentiation into hyaline (arrows) and enclosed chlorophyllose cells (arrow heads) of similar size. e: Transverse section (orthoslice xy0550) of shoot apex with several leaves showing differentiation into hyaline (arrows) and chlorophyllose cells (arrow heads) of similar size. f: Longitudinal section (orthoslice yz0258) of shoot apex with leaves. g: Longitudinal section and partial surface view (orthoslice xz0430) of leaf showing chlorophyllose cells and also hyaline cells, some with transverse fibrils. Specimens, Catefica 49-S156535 (a, e; holotype), Catefica 49-S156534 (b, c, f, g), Catefica 49-S107796 (d). Scale bars = 500 μm (a, b, f), 100 μm (c, d), 200 μm (e, g).

and upper cells of the lamellae that are thin-walled or only slightly thickened distally.

Distinguishing features. *Polytrichastrum incurvum* differs from all extant species of *Polytrichastrum* in having thin-walled or only slightly distally thickened upper cells of the lamella. Among fossil taxa, *P. incurvum* differs from the gametophytes associated with *Eopolytrichum antiquum* KONOPKA, HEREND., G.L.MERR. et P.R.CRANE, which is of Late Cretaceous (Santonian-Campanian) age (Konopka et al. 1997), in having widely incurved marginal laminae in the leaf limb. *Meantoinia alophosioides* BIPPUS, STOCKEY, G.W.ROTHWELL et TOMESCU, which is of Early

Cretaceous (Valanginian) age (Bippus et al. 2017), differs in having lower leaf lamellae that are 2–3 cells high (rather than 3–4(–5) cells high in *P. incurvum*), also in having a distinctly mammillose adaxial lamina surface, in having finely toothed leaf margins, and in lacking the strongly curved lamina margins typical of *P. incurvum*.

Description and Comments on the Material. Three shoot fragments (S174251, S266391, S266392) are known of which the largest is ca. 2.5 mm long. The stem is compressed, and details are not visible except that the cortex consists of 1(–2) layers of incrassate cells which are much smaller than the cells toward the center



Text-fig. 2. Synchrotron radiation X-ray tomographic microscopy (SRXTM) images (volume renderings, a, b; orthoslices, c, d) of a shoot and leaves of *Chlorosphagnum cateficense* HEDENÄS, BOMFLEUR et E.M.FRIIS from the Early Cretaceous Catefica mesofossil flora, Almargem Formation, Portugal. a, b: Both sides of a shoot apex showing several leaves with chlorophyllose cells (arrows) and hyaline cells, some with transverse fibrils (arrow heads). c: Transverse section (orthoslice xy0950) of shoot apex showing differentiation into hyaline (arrows) and chlorophyllose cells (arrow heads) of similar size. d: Longitudinal section (orthoslice yz0682) of shoot apex showing several leaves with chlorophyllose (arrows) and hyaline cells, some with transverse fibrils (arrow heads). Specimen, Catefica 49-S266380 (a–d). Scale bars = 500 μm (a, b), 100 μm (c, d).

of the stem. The leaves are erect on the stem with their distal portions incurved (Text-figs 3a, 4a, b). From a broad sheathing base, each leaf narrows to a limb that gradually narrows further in its upper portion to a cucullate, obtuse apex (Text-figs 3a, 4a, b). The costa is broad and somewhat narrower in the sheathing portion of the leaf. In the limb, the costa has an abaxial epidermis of broader cells with thick outer walls, one layer of guide cells ca. 8–13 μm in diameter, and 3–6 layers of abaxial stereids and 0–2 layers of adaxial stereids ca. 2–4 μm in diameter. On the adaxial leaf surface the costa is covered with straight leaf lamellae. Near the leaf apex there are 3–4 lamellae, farther down there are between 11–17(–20) lamellae (Text-figs. 3b–e, 4c). The lamellae are mostly 3–4 cells high, occasionally up to 5(–6) cells high, with the upper cells thin-walled or slightly thickened. The leaf lamina is unistratose, but towards the costa can be occasionally or entirely bistratose. In the limb, the leaf lamina is broadly incurved over the lateral lamellae (Text-figs 3b, c, 4b). The leaf margin is entire or slightly uneven, but not dentate or denticulate. The lamina cells of the sheathing portion of the leaf are linear, whereas they are irregularly rectangular or quadrate in the transition to the leaf limb and above.

Systematic Relationships. Extant Polytrichales comprise about 19 extant genera, most of which have photosynthetic lamellae on the upper leaf surface. In gametophyte features, *Polytrichastrum* is similar to *Polytrichum* HEDW., from which it differs mainly in sporophytic characters (Bell and Hyvönen 2010). However,

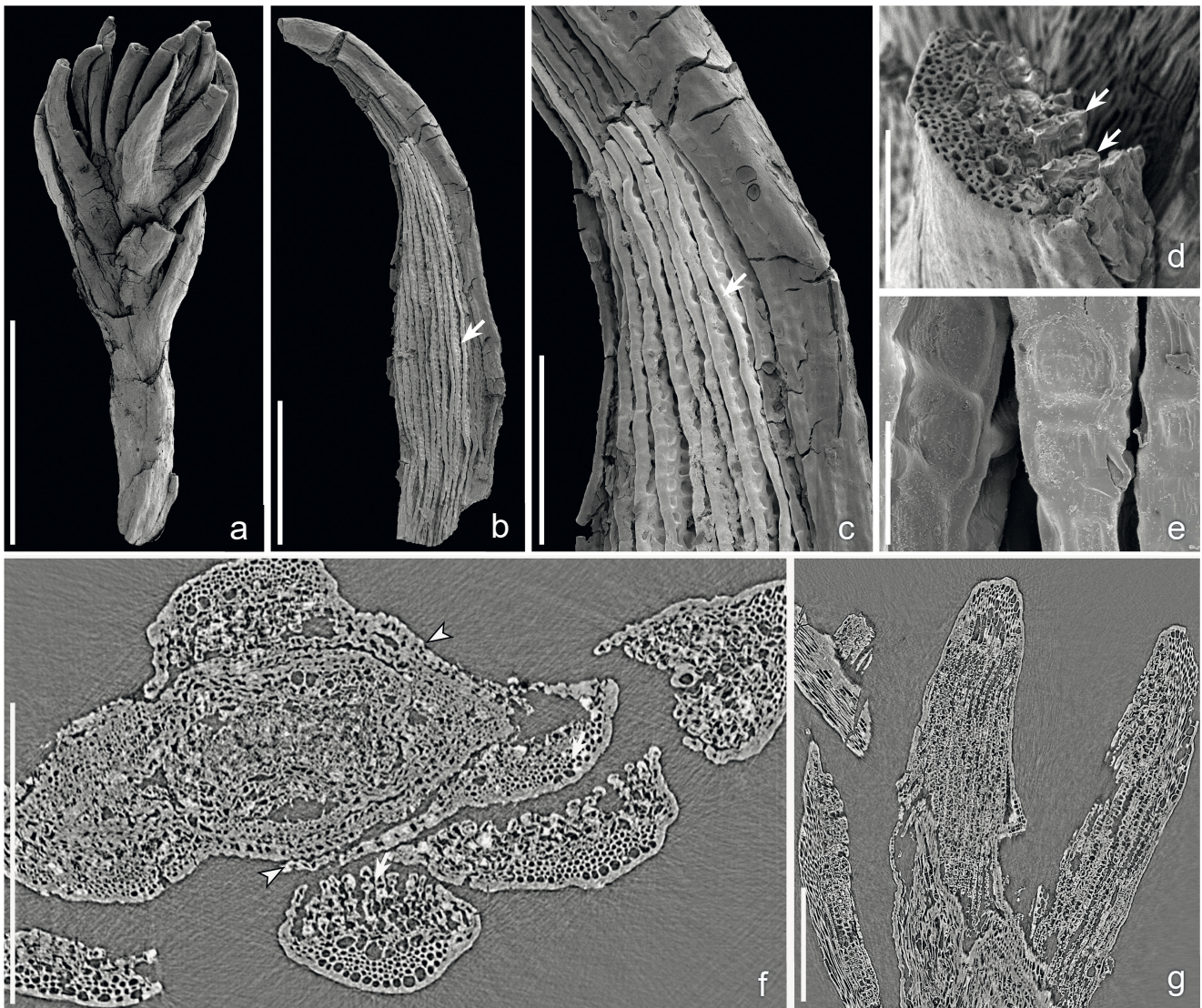
our species is referred to *Polytrichastrum* due to its unique similarity to *Polytrichastrum sexangulare* (FLÖRKE ex BRID.) G.L.SM. and some phenotypes of what has been called '*P. norvegicum* (HEDW.) SCHLJAKOV' (nomenclature unclear) in regard to the incurved leaf margins. This feature is not found in *Polytrichum* and therefore we do not hesitate to place our fossil species in *Polytrichastrum*.

Polytrichastrum incurvum has leaves smaller than many extant species of Polytrichaceae, which may have shoots up to several decimetres tall and well-developed leaves of more than a centimetre long. However, the size of the leaves of *P. incurvum* are well within the range seen among young leaves of the extant species. Assignments to extant genera have also been adopted in systematic treatments of other fossil bryophytes (e.g., Konopka et al. 1998, Bippus et al. 2021) For example, both *Campylopodium allonense* KONOPKA, HEREND. et P.R.CRANE (Konopka et al. 1998) and *Cynodontium luthii* Bippus, G.W.ROTHWELL et STOCKEY (Bippus et al. 2021) were accepted as members of extant genera in the recent overview by Ignatov and Maslova (2021).

Class Bryopsida McCLATCHIE, 1897
Order Diphysciales M.FLEISCH., 1908
Family Diphysciaceae M.FLEISCH., 1919

**Genus *Physcidium* HEDENÄS, BOMFLEUR
 et E.M.FRIIS gen. nov.**

Type species. *Physcidium tortuosum* HEDENÄS, BOMFLEUR et E.M.FRIIS



Text-fig. 3. Scanning electron microscope (SEM, a–e) and synchrotron radiation X-ray tomographic microscopy (SRXTM, f–g) images of a shoot and leaves of *Polytrichastrum incurvum* HEDENÄS, BOMFLEUR et E.M.FRIS from the Early Cretaceous Catefica mesofossil flora, Almargem Formation, Portugal. **a:** Shoot apex showing several incurved leaves. **b:** Leaf showing ventral longitudinal lamellae (arrow) and incurved leaf margins. **c:** Detail of longitudinal lamellae on the ventral leaf surface (arrow) and the incurved leaf margin. **d:** Transverse fracture through the upper portion of leaf showing lamellae on the ventral surface (arrows). **e:** Detail of upper surface of three longitudinal lamellae showing outlines of individual cells. **f:** Transverse section (orthoslice xy0655) of shoot and several leaves at different levels. Note the lamellae on the ventral surface over the costa in sections in the distal part of the leaf (arrow) and the mostly unistratose leaf lamina with smooth cells (arrowheads) and lacking lamellae in the proximal part of the leaf. **g:** Longitudinal section (orthoslice yz1435) showing shoot with several leaves. Specimen, Catefica 49-S174251 (a–g; holotype). Scale bars = 1 mm (a), 200 μ m (b, f, g), 100 μ m (c), 50 μ m (d), 10 μ m (e).

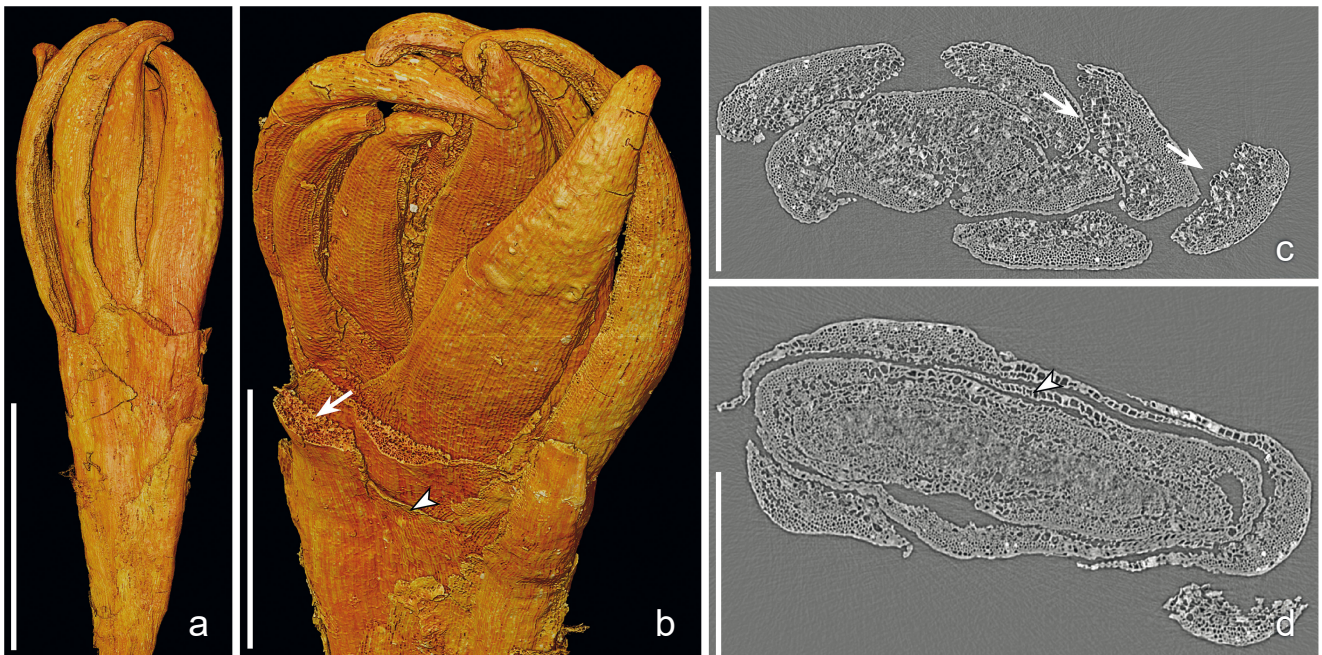
Plant Fossil Names Registry Number.
PFN003146.

Etymology. The name is an anagram of *Diphyscium* D.MOHR, 1803, an extant moss genus, and is chosen to indicate strong resemblance to the gametophyte of the extant genus.

Generic diagnosis. Leaves with an oblong basal portion narrowing above to become linear, long, narrow and parallel-sided, with a shortly narrowed to obtuse or rounded apex. Costa occupying 25–35 % of leaf width. Costa with 1–2 layers of guide cells, only abaxial stereids, or both abaxial and adaxial stereids, and an epidermis that may or

may not be differentiated. Upper leaf lamina 2–4-stratose, cells papillose. Cells of basal lamina sometimes partly inflated.

Distinguishing features. Similar to modern *Diphyscium*, but with a 1–2-stratose basal lamina and basal leaf cells that may be partly inflated. The leaves of *Physcidium* species are also smaller, 1–2 mm long, whereas in most *Diphyscium* species the vegetative leaves are typically larger and 3–7 mm long. The few extant species of *Diphyscium* with shorter leaves lack inflated basal cells. In addition, their costa has either more numerous layers of adaxial stereids or the stereids and guide cells are poorly differentiated.



Text-fig. 4. Synchrotron radiation X-ray tomographic microscopy (SRXTM) images (volume renderings, a, b; orthoslices, c, d) of a shoot and leaves of *Polytrichastrum incurvum* HEDENÄS, BOMFLEUR et E.M.FRIIS from the Early Cretaceous Catefica mesofossil flora, Almargem Formation, Portugal. a, b: Shoot apex showing incurved leaves with distinctly incurved leaf margins. Note a section through the proximal part of a leaf (b) showing lamellae (arrow) over the costa and the unistratose leaf lamina (arrow head). c: Transverse section (orthoslice xy1440) of a shoot showing sections through the distal portions of six leaves showing the distinct lamellae (arrows). d: Transverse section (orthoslice xy2160) of a shoot showing sections through the proximal portions of several leaves showing the unistratose leaf lamina (arrow) with smooth cells. Specimen, Catefica 49-S266392 (a–d). Scale bars = 1 mm (a), 500 μm (b), 200 μm (c, d).

***Physcidium tortuosum* HEDENÄS, BOMFLEUR
et E.M. FRIIS sp. nov.**

Text-fig. 5a–f

Holotype. S266387 (Catefica sample 49; figured Text-fig. 5a, b).

Plant Fossil Names Registry Number. PFN003147.

Paratypes. S266375, S266388, S266389, S266390 [Catefica sample 49; figured Text-fig. 5c, f (S266389); Text-fig. 5d, e (S266390)].

Repository. Palaeobotanical Collections, Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden.

Etymology. The specific epithet refers to the conspicuously twisted leaves.

Type locality. Catefica (39° 03' 30" N, 09° 14' 30" W), between the villages of Catefica and Mugideira, about 4 km south of Torres Vedras, Portugal.

Type stratum and age. Almargem Formation, Early Cretaceous (Aptian–early Albian).

Specific diagnosis. Leaves from erect or weakly patent base strongly incurved. Costa occupying 30–35 % of leaf width, with numerous layers of abaxial and often a few of adaxial stereids.

Distinguishing features. *Physcidium tortuosum* differs from *P. simsimiae* HEDENÄS, BOMFLEUR et E.M.FRIIS, the

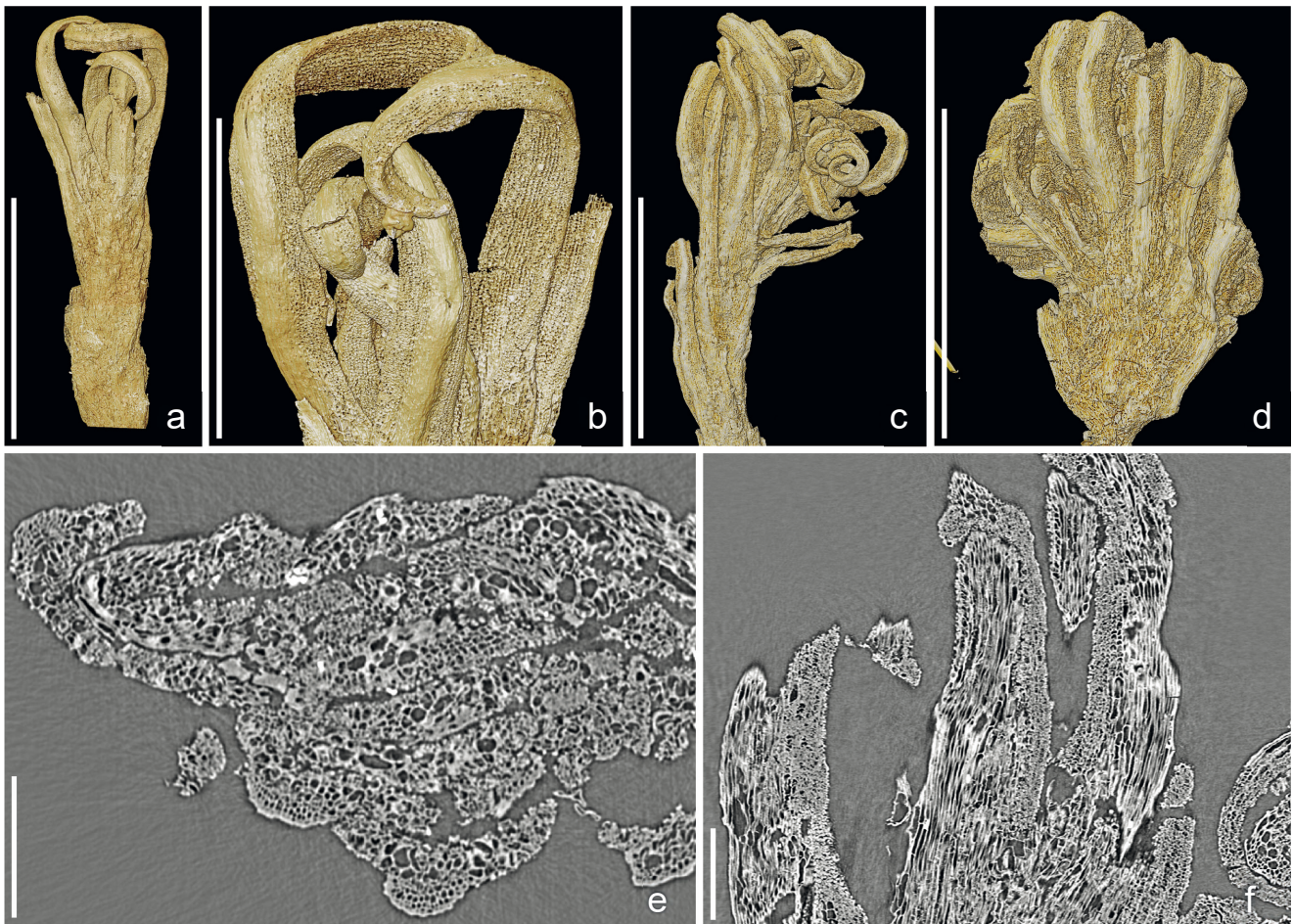
other species of the genus in the Catefica mesofossil flora, in the strongly incurved upper portions of the leaves, and a broader costa that occupies 30–35 % of the leaf width. There are also a larger number of abaxial stereids and few adaxial stereids.

Description and Comments on the Material. Five shoot fragments (S266375, S266387, S266388, S266389, S266390) up to ca. 2.0 mm long are known. They bear leaves that are strongly incurved in their upper portion. Leaves are 1.5–2 mm long (Text-fig. 5a–d) with an oblong leaf base, and a long, linear, parallel-sided upper portion that narrows abruptly into an obtuse or rounded apex. The costa is well developed and occupies 30–35 % of the leaf width. It has 1–2 layers of guide cells, 3–4(–5) layers of abaxial stereids, 1(–2) layers of adaxial stereids, and sometimes an indistinct partial abaxial epidermis (Text-fig. 5e). Cells of the adaxial costa are similar to cells of the lamina, whereas the cells of the abaxial costa are longer and clearly differentiated from those of the lamina. The basal leaf lamina is 1(–2)-stratose with partly inflated cells towards the costa. The leaf lamina in the upper leaf is (2–)3–4-stratose (Text-fig. 5e, f), and in at least some portions its cells have low to moderately high papillae (Text-fig. 5e).

***Physcidium simsimiae* HEDENÄS, BOMFLEUR
et E.M. FRIIS sp. nov.**

Text-fig. 6a–e

Holotype. S266378 (Catefica sample 49; figured Text-fig. 6a–c).



Text-fig. 5. Synchrotron radiation X-ray tomographic microscopy (SRXTM) images (volume renderings, a–d; orthoslices, e, f) of shoots and leaves of *Physcidium tortuosum* HEDENÄS, BOMFLEUR et E.M.FRIIS from the Early Cretaceous Catefica mesofossil flora, Almagem Formation, Portugal. a–d: Shoot apices showing leaves with typical incurved upper portions. e: Transverse section (orthoslice xy0660) of shoot showing several leaves with a 3–4-stratose leaf lamina with partly papillose cells on the dorsal surface. f: Longitudinal section (orthoslice yz0363) through a shoot apex with several leaves showing portions of costae and with elongate cells and laminae with short cells. Specimens, Catefica 49-S266387 (a, b; holotype), Catefica 49-S266389 (c, f), Catefica 49-S266390 (d, e). Scale bars = 1 mm (a–d), 100 μm (e, f).

Plant Fossil Names Registry Number.
PFN003148.

Paratypes. S266369, S266379 [Catefica sample 49; figured Text-fig. 6d–e (S266379)].

Repository. Palaeobotanical Collections, Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden.

Etymology. The specific epithet is chosen in reference to Maria Manuela Pinheiro Sim-Sim in honour of her contributions to the bryology of the Iberian Peninsula.

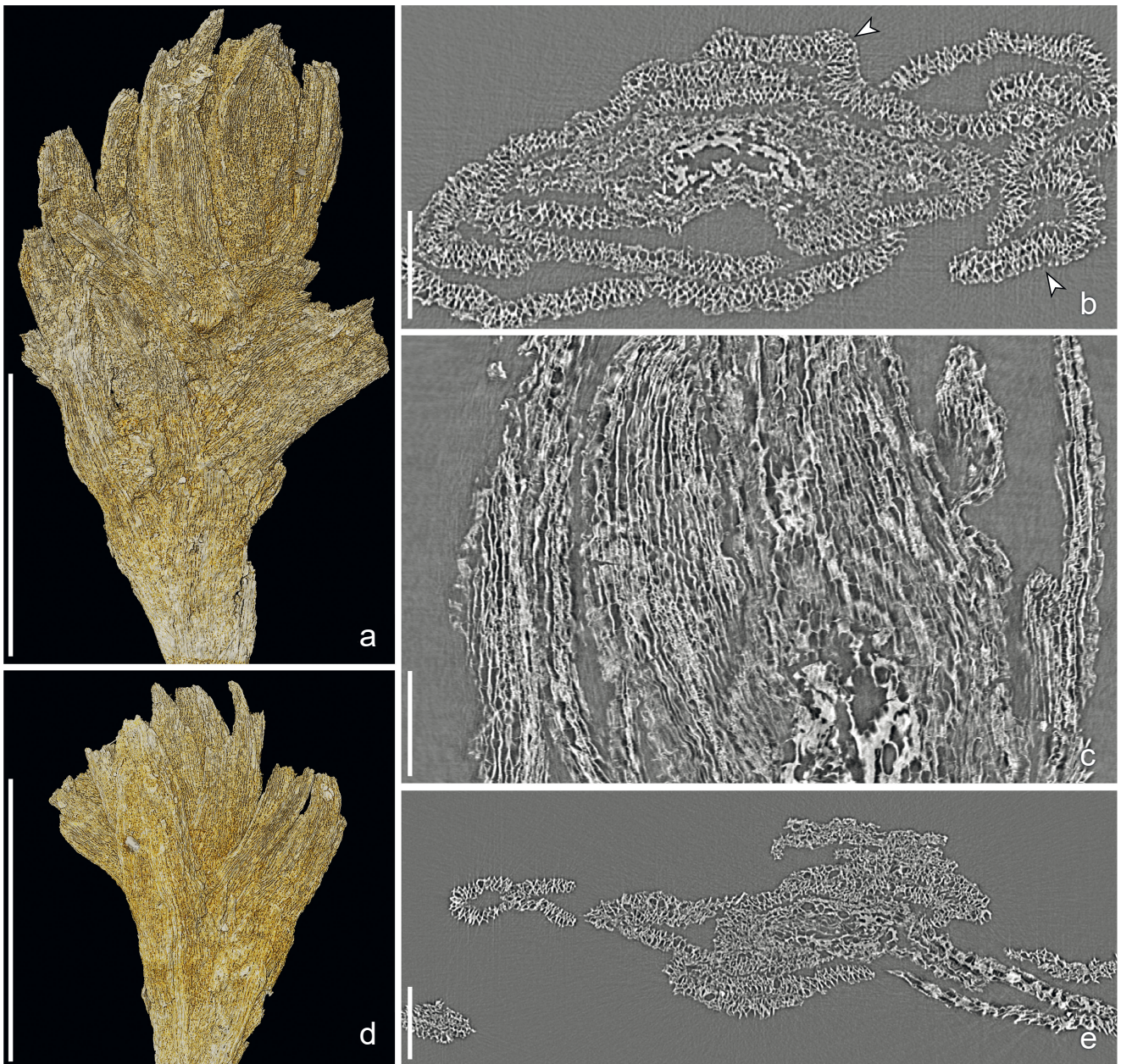
Type locality. Catefica (39° 03' 30" N, 09° 14' 30" W), between the villages of Catefica and Mugideira, about 4 km south of Torres Vedras, Portugal.

Type stratum and age. Almagem Formation, Early Cretaceous (Aptian–early Albian).

Specific diagnosis. Leaves straight and erect, or at best weakly curved inwards. Costa occupying ca. 25 % of leaf width, with few layers of abaxial stereids.

Distinguishing features. *Physcidium simsimiae* differs from *P. tortuosum*, the other species of the genus, in the almost erect or slightly curved upper portions of the leaves, and the narrower costa that occupies ca. 25 % of the leaf width. There are also fewer abaxial stereids and no adaxial stereids.

Description and Comments on the Material. The three shoot fragments (S266378, S266369, S266379) are up to ca. 2.0 mm long. The leaves are mostly broken but are straight, or at most slightly curved (Text-fig. 6a, d). Leaves are estimated to have been 1.5–2 mm long (Text-fig. 6a, d), with an oblong leaf base and a linear upper portion. The apical portions of the leaves are missing in the fossils. The costa is well developed and occupies ca. 25 % of the leaf width. It has 1–2 layers of guide cells, (1–)2–3 layers of abaxial stereids, and an indistinctly differentiated adaxial epidermis (Text-fig. 6b, c). Cells of the adaxial costa are similar to cells of the lamina, whereas cells of the abaxial costa are longer and clearly differentiated from those of the lamina. The basal leaf lamina is 2-stratose with some cells



Text-fig. 6. Synchrotron radiation X-ray tomographic microscopy (SRXTM) images (volume renderings, a, d; orthoslices, b, c, e) of shoots and leaves of *Physcidium simsimiae* HEDENÄS, BOMFLEUR et E.M.FRIIS from the Early Cretaceous Catefica mesofossil flora, Almargem Formation, Portugal. a, d: Shoot apices with several leaves. b, e: Transverse sections (orthoslices xy0879, xy0657) of shoots with several leaves. Note the 2–3-stratose leaf lamina with partly papillose cells on the dorsal surface and narrow weakly differentiated costa (arrow heads in b). c: Longitudinal section near a shoot apex showing several leaves (orthoslice yz0540). Specimens, Catefica 49-S266378 (a–c; holotype), Catefica 49-S266379 (d, e). Scale bars = 1 mm (a, d), 100 µm (b, c, e).

that are slightly inflated. Cells of the upper leaf lamina are 2–3-stratose throughout, with cells in at least in some portions with low or moderately high papillae (Text-fig. 6b, e).

Systematic Relationships. The new genus *Physcidium* is clearly referable to the Diphysciales based on the strong costa and the weakly differentiated basal leaf lamina that narrows above into a long, linear, parallel-sided upper portion, very similar to leaves of modern *Diphyscium* (Magombo 2003). The anatomy of the costa and the 2–4-stratose upper leaf lamina in both species also fit within the variation of modern *Diphyscium*. Both species differ from modern *Diphyscium*, however, in having somewhat

inflated cells in their basal portion and in having a partly or entirely bistratose basal leaf lamina, whereas the basal leaf lamina is strictly unistratose in *Diphyscium*. In these features, *Physcidium* is somewhat reminiscent of the genus *Alophosia* CARDOT (Polytrichaceae), which lacks lamellae and has distinctly mammillose cells on only the adaxial leaf surface (Smith 1971).

Order Dicranales M.FLEISCH., 1920
Family Leucobryaceae SCHIMP., 1856

Three species of Leucobryaceae are recognized and assigned to two extant genera and one extinct genus (Text-

figs 7, 8a–i). There is an additional specimen (S266386, Text-fig. 8j–m) also attributable to Leucobryaceae, but for which the leaf sections are not sufficiently clear for assignment to a genus of the family.

Genus *Dicranodontium* BRUCH et SCHIMP., 1847

***Dicranodontium minutum* HEDENÄS, BOMFLEUR et E.M.**

FRIIS sp. nov.

Text-fig. 7 a–d

Holotype. S266382 (Catefica sample 49; figured Text-fig. 7a, c).

Plant Fossil Names Registry Number. PFN003149.

Paratype. S266384 (Catefica sample 49; figured Text-fig. 7b, d).

Repository. Palaeobotanical Collections, Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden.

Etymology. The epithet refers to the small size.

Type locality. Catefica (39° 03' 30" N, 09° 14' 30" W), between the villages of Catefica and Mugideira, about 4 km south of Torres Vedras, Portugal.

Type stratum and age. Almagem Formation, Early Cretaceous (Aptian–early Albian).

Specific diagnosis. A member of the genus *Dicranodontium*, but with leaves much smaller than those of any extant species.

Distinguishing features. Leaves of *Dicranodontium minutum* are up to 1.9 mm long, much smaller than the leaves of any extant species, which are at least 4 mm long and may be up to 12 mm long. Leaves have a very broad costa that occupies about half the leaf width at the base of the leaf and that fills the acumen almost completely. Leaves have a well-developed epidermis on both the adaxial and abaxial side, with one layer of large guide cells, and multiple layers of both adaxial and abaxial stereids.

Description and Comments on the Material. The two shoot fragments (S266382, S266384) are up to ca. 2.0 mm long, with long and narrow leaves that are up to 1.9 mm long based on estimates of the length of the broken leaf apices (Text-fig 7a, b). Costa very broad, occupying about half the leaf width in the basal leaf portion, most of the acumen above, and the entire acumen near the leaf apex. The costa has a well-differentiated epidermis on both the abaxial and adaxial sides, with enlarged, sometimes partly collapsed, epidermal cells (Text-fig. 7c, d). There is one layer of large guide cells, and multiple layers of both adaxial and abaxial stereids (Text-fig. 7c, d). Cells of the upper leaf lamina are elongate or (elongate-) rectangular.

Systematic relationships. The order Dicranales comprises about 15 families within which the

fossil material most closely resembles the extant genus *Dicranodontium*, one of twelve genera currently recognized in the Leucobryaceae. The fossil material is so closely similar to living *Dicranodontium* in leaf shape and costa width and anatomy that it can be readily assigned to the extant genus. The fossil material is smaller in size than any extant species of *Dicranodontium*, where shoots may be 5–10 cm tall and have leaves up to 4–12 mm long. However, the fossil material is otherwise similar to some extant species in the long and narrow leaves with a broad costa, and in details of costa anatomy (Frahm 1997, Bonfim Santos and Stech 2017). *Dicranodontium* differs from extant *Dicranum* HEDW. species with a broad costa by a distinctly differentiated long subula, and elongate cells of the upper leaf lamina. Among genera of Leucobryaceae the well differentiated epidermis on both the adaxial and abaxial sides of the costa distinguishes the fossils from species of *Atractyllocarpus* MITT., which have only abaxial stereids (Bonfim Santos and Stech 2017), and from species of *Campylopus* BRID., which have only a single layer of adaxial stereids and also a shorter subula in relation to the basal portion of the leaf.

An important consideration for *Dicranodontium minutum* is whether the minute size of the fossils is considered conspicuous enough to serve as a species-diagnostic criterion, given that only the apical-most portions of the fossil shoots are preserved and that shrinkage may also have occurred during charcoalification. It is possible that only the apical portions of the gametophytes were sufficiently protected from the fire, perhaps by the surrounding leaves, and hence became charcoaled rather than completely burnt to ash (cf., Li et al. 2022a). Experimental charcoalification has shown to reduce the size of plant organs between 14 and 47 %, depending on the organ type (Lupia 1995). However, this is much less than the difference between the fossils and their morphologically modern counterparts, and thus seems unlikely to account fully for the size differences. In addition, the single spore capsule recovered and the *Physcidium* shoot fragments, have sizes that are more in agreement with those of modern mosses.

Genus *Campylopus* BRID., 1818

***Campylopus lusitanicus* HEDENÄS, BOMFLEUR
et E.M.FRIIS sp. nov.**

Text-fig. 7e–h

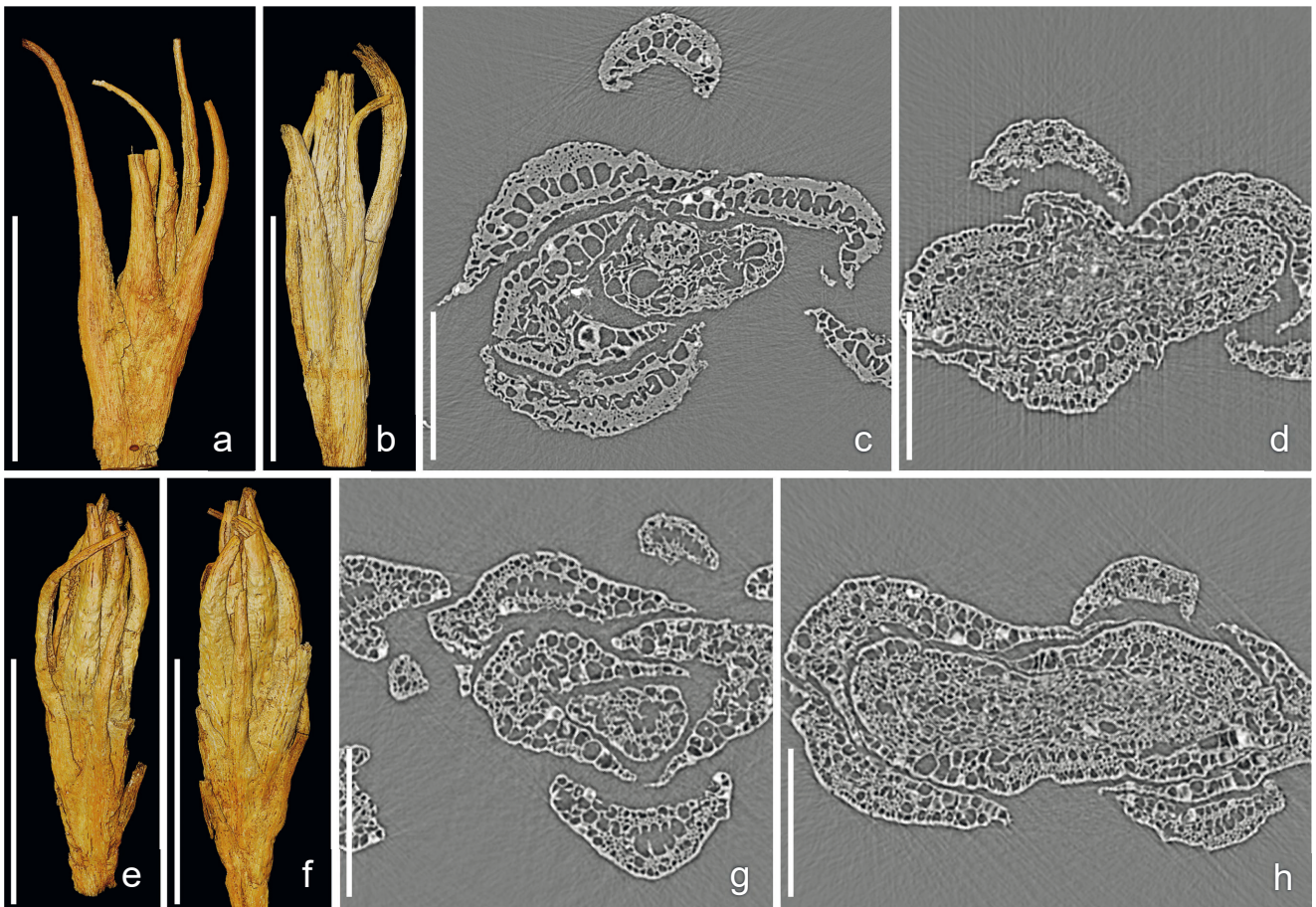
Holotype. S266385 (Catefica sample 49; figured Text-fig. 7e–h).

Plant Fossil Names Registry Number. PFN003150.

Paratype. S266383 (Catefica sample 49).

Repository. Palaeobotanical Collections, Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden.

Etymology. The species epithet refers to the Latin name of Portugal where the fossils were discovered.



Text-fig. 7. Synchrotron radiation X-ray tomographic microscopy (SRXTM) images (volume renderings, a, b, e, f; orthoslices, c, d, g, h) from shoots of *Dicranodontium minutum* HEDENÄS, BOMFLEUR et E.M.FRIIS (a–d) and *Campylopus lusitanicus* HEDENÄS, BOMFLEUR et E.M.FRIIS (e–h) from the Early Cretaceous Catefica mesofossil flora, Almargem Formation, Portugal. a, b: Shoot apices with several leaves showing the broad costa comprising almost the full width of the leaf. c, d: Transverse sections (orthoslices xy2925, xy1725) of leaves near the shoot apices showing the broad costa. Note the prominently expanded guide cells with several layers of stereids on both their dorsal and ventral sides, especially distinct in (c). e, f: Shoot apex with several leaves showing the broad costa. g, h: Transverse sections (orthoslices xy0867, xy1675) of leaves near the shoot apices showing the expanded guide cells with uniformly unistratose stereids on their ventral side. Specimens, *D. minutum*, Catefica 49-S266382 (a, c; holotype), Catefica 49-S266384 (b, d); *C. lusitanicus* Catefica 49-S266385 (e–h; holotype). Scale bars = 1 mm (a, b, e, f), 100 μ m (c, d, g, h).

Type locality. Catefica (39° 03' 30" N, 09° 14' 30" W), between the villages of Catefica and Mugideira, about 4 km south of Torres Vedras, Portugal.

Type stratum and age. Almargem Formation, Early Cretaceous (Aptian–early Albian).

Specific diagnosis. A member of the genus *Campylopus*, but with leaves that are much smaller than those of any extant species.

Distinguishing features. The leaves of *Campylopus lusitanicus* are up to 1.6 mm long, much smaller than the leaves of any extant species, which are at least 3 mm and up to ca. 10 mm long. Leaves have a very broad costa that occupies about half the leaf width at the base of the leaf and that fills out the acumen almost completely. Leaves have a well-developed epidermis on both the adaxial and abaxial sides, with one layer of large guide cells and multiple layers of abaxial stereids, but only a single layer of adaxial stereids.

Description and Comments on the Material. Specimens S266383 and S266385 are shoot

fragments up to ca. 2.0 mm long (length of broken leaf apices estimated), with leaves that are up to 1.6 mm long. Leaves have a broad costa that occupies about half the leaf width in the basal leaf portion and most of the acumen (Text-fig. 7e, f). The epidermis of the costa is well differentiated on both the adaxial and abaxial sides with enlarged epidermal cells (Text-fig. 7g, h). There is one layer of large guide cells, multiple layers of abaxial stereids, and a single layer of adaxial stereids (Text-fig. 7g, h). The acumen consists entirely of the costa; a lamina is lacking.

Systematic relationships. The fossil material is so similar to the extant *Campylopus* that it can be readily assigned to that genus. *Campylopus*, like *Dicranodontium*, is one of twelve genera of Leucobryaceae. Like in many extant *Campylopus* species, our fossil has long and narrow leaves with a broad costa, but the leaves in the fossils are much smaller (Bonfim Santos and Stech 2017). As in the case of *Dicranodontium minutum* we think it unlikely that the small leaf size of *Campylopus lusitanicus* reflects shrinkage during preservation. The epidermis is well differentiated on both

abaxial and adaxial sides, with enlarged epidermal cells, one layer of large guide cells, multiple layers of abaxial stereids, and a single layer of adaxial stereids (cf., Frahm 1997). The latter distinguishes *Campylopus* from *Dicranodontium*, including *D. minutum* described above, which has multiple layers of adaxial stereids. The acumen consists entirely of the costa and a lamina is entirely lacking. The costa in *Campylopus* is broader than in *Microcampylopus* (MÜLL.HAL.) M.FLEISCH. It is also broader than in species of *Campylopodium* (MÜLL.HAL.) BESCH. where the costa occupies about one third of the leaf base. The genus *Campylopus* is widely distributed globally (Stech and Wagner 2005).

**Genus *Canaliculidium* HEDENÄS, BOMFLEUR
et E.M. FRIIS gen. nov.**

Type species. *Canaliculidium fissuratum* HEDENÄS, BOMFLEUR et E.M. FRIIS

Plant Fossil Names Registry Number. PFN003151.

Etymology. From Latin *canaliculus*, small gutter. The name refers to the longitudinal groove of the abaxial costa.

Generic diagnosis. Leaves with a narrowly ovate base that narrows gradually towards leaf apex. Costa poorly differentiated, occupying more than half of the leaf width in the leaf base. Abaxial surface of the costa with a median longitudinal groove.

Distinguishing features. The distinct median longitudinal groove on the abaxial surface of the costa, and the relatively poorly differentiated anatomy of the costa, set *Canaliculidium* apart from all other genera of Leucobryaceae.

***Canaliculidium fissuratum* HEDENÄS, BOMFLEUR
et E.M. FRIIS sp. nov.**

Text-fig. 8a–i

Holotype. S171522 (Catefica sample 49; figured Text-fig. 8a–c).

Plant Fossil Names Registry Number. PFN003152.

Paratypes. S266374, S266376, S266416 [Catefica sample 49; figured Text-fig. 8d–f (S266374); Text-fig. 8g–i (S266376)].

Repository. Palaeobotanical Collections, Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden.

Etymology. The specific epithet refers to the fissure-like appearance of the longitudinal groove of the abaxial costa when viewed in transverse section.

Type locality. Catefica (39° 03' 30" N, 09° 14' 30" W), between the villages of Catefica and Mugideira, about 4 km south of Torres Vedras, Portugal.

Type stratum and age. Almargem Formation, Early Cretaceous (Aptian–early Albian).

Specific diagnosis. Leaves with a narrowly ovate base that narrows gradually towards leaf apex. Costa occupying 50–70 % of the leaf width in the leaf base. In transverse section median longitudinal groove seen as a fissure or depression penetrating to one third to one half of the thickness of the costa. Costa with one layer of guide cells. Cells above and below guide cells thin-walled or partly slightly incrassate. Cells of the epidermis not differentiated from the internal cells of the costa.

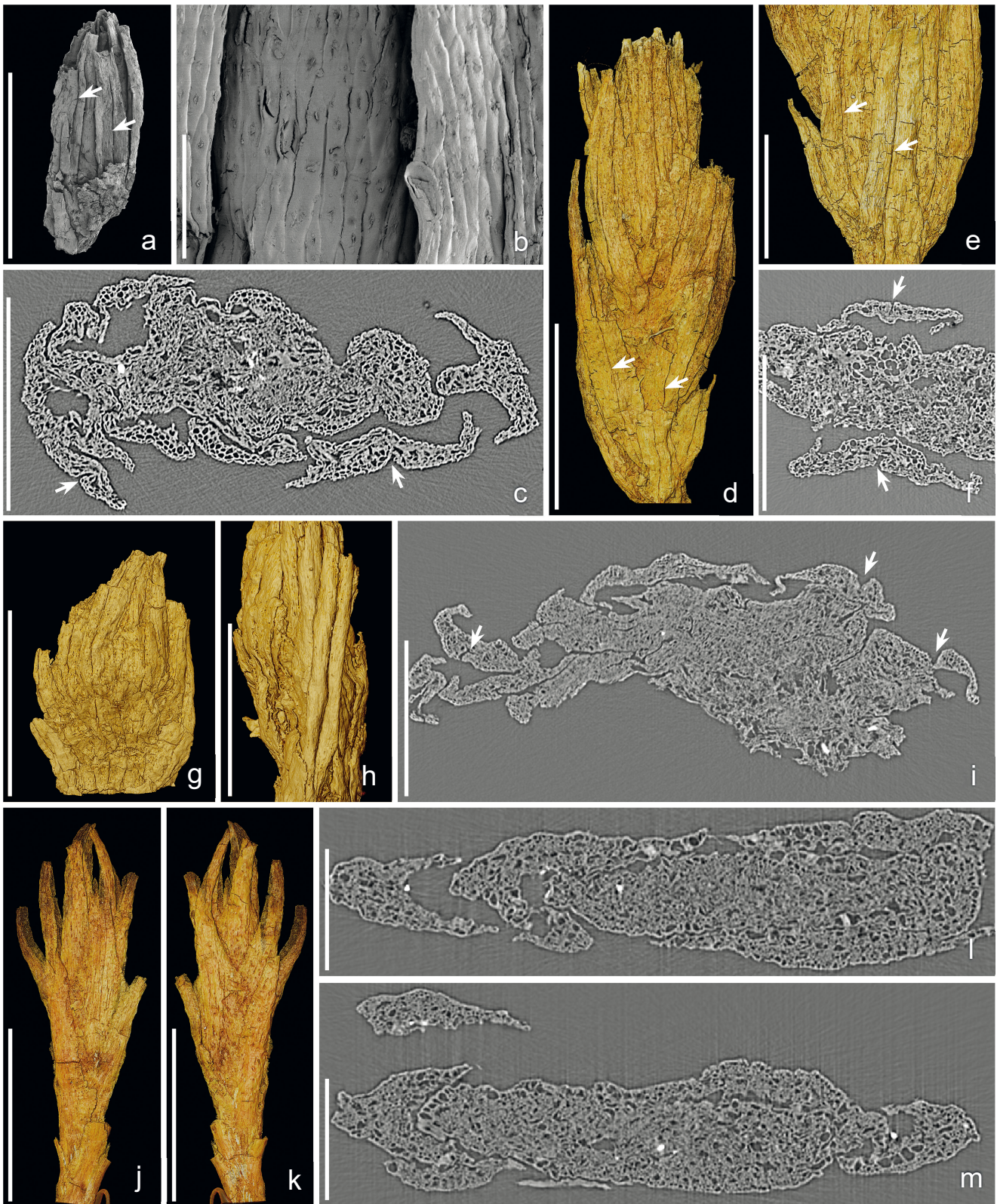
Distinguishing features. This is the only known species of *Canaliculidium* and the distinguishing features are the same as for the genus.

Description and Comments on the Material. The three shoot fragments (S171522, S266376, S266416) of *Canaliculidium fissuratum* are up to 1.2–2.5 mm long. The leaves gradually narrow upwards from a narrowly ovate base (Text-fig. 8a, d, e, g, h). One almost complete leaf with only the most apical portion missing is ca. 2 mm long. Leaves have a costa that occupies 50–70 % of the leaf width at the leaf base, and ca. 70 % of the leaf width in the apical part of the leaf. Near the leaf base, the leaf lamina is unistratose. In the apical part of the leaf the lamina is bistratose. On the abaxial surface of the costa, large portions are irregularly pitted (Text-fig. 8b). In transverse section the costa has one layer of guide cells (Text-fig. 8c, f). The cells above and below are thin-walled or partly slightly incrassate, and do not form clear layers of stereids or a clearly differentiated epidermis. In a near median position on the abaxial surface of the costa there is a distinct longitudinal groove (Text-fig. 8a, d, e, g, h). In transverse section this longitudinal groove is seen as a fissure or depression that penetrates to one third to one half of the costa thickness (Text-fig. 8c, f, i). The distinguishing features of the costa are visible in all three samples, but the details of the costal structure are best preserved in S171522, and this is here selected as the holotype of the name.

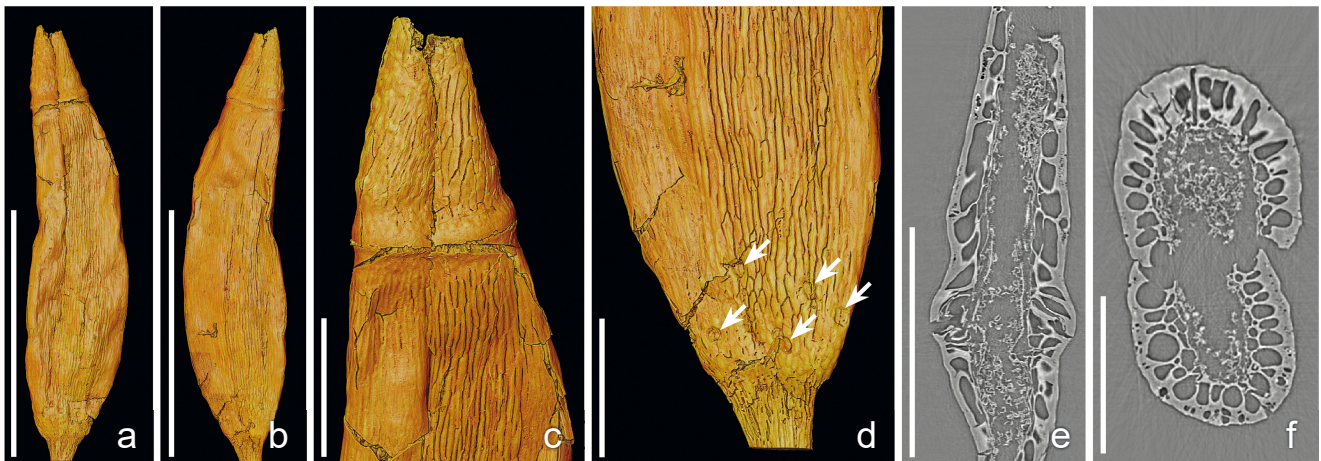
Systematic relationships. *Canaliculidium* is conclusively assignable to the order Dicranales and the family Leucobryaceae based on its similarity in many features to many extant Leucobryaceae; the long and narrow leaves and the strong and broad costa are similar to, for example, *Campylopus* or *Dicranodontium*. These features are typical of most non-leucobryoid members of the family, where costal anatomy varies significantly (Bonfim Santos and Stech 2017). However, the distinct fissure in the abaxial surface distinguishes it from any extant or fossil genus.

cf. Ditrichaceae LIMPR.

In addition to the fragments of moss shoots described above a single spore capsule (S266084, fig. 9) is known but cannot be linked to any of the vegetative remains. The spore capsule is 1.7 mm long, including 0.2 mm remaining of the



Text-fig. 8. Scanning electron microscope (SEM, a, b) and synchrotron radiation X-ray tomographic microscopy (SRXTM) images (volume renderings, d, e, g, h, j, k; orthoslices, c, f, i, l, m) from shoots of *Canaliculidium fissuratum* HEDENÄS, BOMFLEUR et E.M.FRIIS (a–i) and undetermined Leucobryaceae sp. (j–m) from the Early Cretaceous Catefica mesofossil flora, Almargem Formation, Portugal. a, d, e, g, h: Shoot apices with leaves. Note the longitudinal furrow in the middle of dorsal surface of the costa (arrows in a, d, e); b: Detail of dorsal surface of costa showing irregular pits. c, f, i: Transverse sections (orthoslices xy2000, xy3560, xy0820) of shoots with leaves showing the furrow in the middle of the dorsal surface of the costa (arrows). j, k: Both sides of shoot apex with leaves showing a broad costa. l, m: Transverse sections (orthoslices xy1360, xy1657) of shoot showing leaves. Specimens, *C. fissuratum*, Catefica 49-S171522 (a–c; holotype), Catefica 49-S266374 (d–f), Catefica 49-S266376 (g–i); Leucobryaceae sp., Catefica 49-S266386 (j–m). Scale bars = 1 mm (a, d, g, j, k), 500 μ m (e, h), 200 μ m (c, f, i), 100 μ m (l, m), 50 μ m (b).



Text-fig. 9. Synchrotron radiation X-ray tomographic microscopy (SRXTM) images (volume renderings, a–d; orthoslices, e, f) of spore capsule of cf. *Ditrichaceae* sp. from the Early Cretaceous Catefica mesofossil flora, Almargem Formation, Portugal. a, b. Both sides of complete spore capsule. c) Detail of distal portion of spore capsule with basal portion of lid remaining. d) Detail of proximal portion of spore capsule showing stomata (arrows). e) Longitudinal section (orthoslice xz1170) through distal portion of spore capsule showing basal portion of lid. f) Transverse section (orthoslice xy0815) through distal portion of spore capsule showing a thick-walled exothecium and the internal unstructured remains of the spore sack with contents. Specimen, Catefica 49-S266084. Scale bars = 1 mm (a, b), 200 μm (c–e), 100 μm (f).

lid (Text-fig. 9a, b). Externally the spore capsule is well preserved (Text-fig. 9a–d) but internal details are unclear (Text-fig. 9e, f). The apex of the operculum is also not present, which precludes more exact systematic placement. Several stomata are present at the base of the spore capsule (Text-fig. 9d), which precludes close relationship with extant *Tetraphis* HEDW., which has spore capsules of similar shape but that lack stomata. The spore capsule certainly belongs to a species of acrocarpous moss and is similar to spore capsules of many members of extant Ditrichaceae or the Pottiaceae. According to Liu et al. (2019) these two families both belong to Dicranales.

Discussion

The Moss Fossil Record and Moss Phylogeny

Amber inclusions have long been the main source of new information on the fossil history of late Mesozoic and Cenozoic mosses because they provide three-dimensional information that is sufficiently well-preserved for close comparison with extant taxa. However, with a few exceptions, most of the richer and more well-studied amber localities that preserve mosses are of Palaeogene or Neogene age. From the Palaeogene, the northern European Baltic amber (e.g., Frahm 2004, 2009, Frahm and Gröhn 2013, Ignatov et al. 2019) and Bitterfeld amber from Germany (e.g., Frahm 2004), together with the Rovno amber from Ukraine (e.g., Frahm 2009, Ignatov and Perkovsky 2011, Ignatov et al. 2016, 2019), the Cambay amber from India (Heinrichs et al. 2016), and the Sakhalin amber from the Russian Far East (Ignatov and Perkovsky 2013), have all been studied intensively. From the Neogene, inclusions in Miocene amber from the Dominican Republic have also been studied in detail (e.g., Frahm 1993, 2001, 2006, 2009) but there are also Neogene amber floras

from elsewhere (e.g., Ethiopian amber, Bouju et al. 2022; Mexican amber, Hernández-Damián et al. 2023; Zhangpu amber, SE China, Feldberg et al. 2023).

Compared to Cenozoic occurrences, records of mosses in Cretaceous age amber are sparse. However, mosses are known from the Myanmar (e.g., Hedenäs et al. 2014, Heinrichs et al. 2014) and Honshu (Katagiri et al. 2013) ambers, both of which are thought to be of Late Cretaceous age. Also important for comparison with the Catefica assemblage are occurrences of charcoaled mosses from the Buffalo Creek Member of the Gaillard Formation at the Allon locality, Georgia, USA (Konopka et al. 1997, 1998), and the permineralized mosses discovered in carbonate concretions along the Pacific coast of British Columbia (Tomescu 2016; see also Bippus et al. 2017, 2021, Tomescu et al. 2018) and the North Slope of Alaska (Bippus et al. 2021). Apart from these exceptional deposits, the fossil record of Cretaceous mosses consists mostly of variably preserved impression or compression fossils, often from rather isolated occurrences including the Russian Far East (Ignatov and Shcherbakov 2011, Mamontov and Ignatov 2019) and Australia (e.g., Drinnan and Chambers 1986). With few exceptions, similar adpression preservation also forms the dominant mode of preservation in the older Mesozoic and the Palaeozoic fossil record of bryophytes (see, e.g., Tomescu et al. 2018).

All modes of preservation that encapsulate systematically informative features are helpful for documenting the evolutionary history of mosses, but it is also important to consider the extent to which the record may be skewed by taphonomic biases. In the case of amber, for example, one prominent effect is the strong overrepresentation of epiphytic, especially corticolous plants (e.g., Bechteler et al. 2017, Heinrichs et al. 2018, Feldberg et al. 2021), including pleurocarpous mosses (e.g., Hedenäs et al. 2014, Li et al. 2022b). Likewise, mesofossil assemblages and mosses

preserved in marine or lacustrine conditions may be prone to systematic biases resulting from the manner in which those accumulations are derived from specific habitats.

Current models of moss phylogeny resolve the Takakiales, Sphagnales, Andraeales, Oedipodiales, Tetraphidales, Polytrichales, Buxbaumiales, Diphysciales, Gigaspermiales, Funariales, Timmiales and Dicranales as successive sister groups to the Bryidae (Liu et al. 2019). The orders in the basal grade of the moss phylogeny comprise about 35 % of the almost 13,000 species of extant mosses, and within the Bryidae the major subgroup, the superorder Hypnanae (pleurocarpous mosses), comprise around half of all moss species (Liu et al. 2019). All the moss fossils from the Catefica mesofossil flora, probably including the single moss capsule, can be assigned to four of the orders that comprise the basal grade of the moss phylogeny.

The charcoaled and lignified mosses from Catefica and the Allon locality, as well as the permineralized mosses from Apple Bay, all present a similar picture, reflecting the presence of taxa from the basal grade of the moss phylogeny. The Allon mosses are assigned to the Polytrichaceae (Polytrichales) and Dicranaceae (Dicranales) based on both gametophytes and sporophytes of Late Cretaceous (Santonian-Campanian) age. Based on well-preserved gametophytes the Apple Bay mosses, which are of Early Cretaceous (Valanginian) age, are assigned to the Polytrichaceae (Polytrichales) and Leucobryaceae (Dicranales) (Tomescu 2016). The permineralized moss described from the North Slope of Alaska is of Late Cretaceous age (Santonian/Campanian – Maastrichtian) and is assigned to the Rhabdoweisiaceae (Dicranales) based on well-preserved gametophytes (Bippus et al. 2021). Among all these fossil assemblages there are so far no records of mosses that can be confidently referred to the Bryidae or to any pleurocarpous lineages other than Tricostaceae, an extinct family of uncertain position within the Hypnanae (Shelton et al. 2015, 2016).

In the Catefica assemblage, *Chlorosphagnum* is of special interest because while it can be assigned conclusively to the Sphagnales, its unique leaf cell dimorphism, with chlorophyll and hyaline cells of similar size, distinguishes it from any extant or fossil genus. The so-far oldest *bona fide* body fossils of *Sphagnum sensu stricto* come from Baltic amber (Frahm 2009) and from Eocene lignites (Riegel and Wilde 2016), although Alexander Bippus, in his doctorate thesis (Bippus 2022), describes and illustrates three new *Sphagnum* species based on structurally preserved gametophytes in carbonate concretions from the Upper Cretaceous (Santonian–Campanian) of Vancouver Island, Canada. In addition to these more complete body fossils, there are several surprisingly modern-looking records of *Sphagnum*-like leaf fragments from rocks of Cretaceous (Arnold 1932, Wilson and Webster 1946), Jurassic (Reissinger 1950), Triassic (Pant and Basu 1976), and even Ordovician (Cardona-Correa et al. 2016) age. While many of these records are considered dubious due to limited sample sizes, ambiguous features, possibility of contamination or

just their exotic occurrence (e.g., Steere 1946, Tomescu et al. 2018, Ignatov and Maslova 2021), there is general agreement that the well-preserved specimens of a single complete and one fragmented *Sphagnum* leaf from the Jurassic of Germany (Reissinger 1950) are reliable records of the genus. Notably, these fragments already show the typical leaf-cell dimorphism with hyaline cells much larger than the chlorophyll cells.

All other well-substantiated pre-Cenozoic occurrences of sphagnopsid body fossils belong to Protosphagnales, an extinct clade characterized by unique leaf architecture and cell pattern (e.g., Neuburg 1960, Ignatov 1990, Hübers and Kerp 2012, Ignatov and Maslova 2021). There is currently no consensus about the precise systematic placement of dispersed *Sphagnum*-like spores – a locally common component in Mesozoic and Cenozoic spore assemblages (e.g., Balme 1995, Traverse 2007); the problem is exacerbated by the lack of information about *in situ* spores of exclusively fossil sphagnopsid taxa.

The unique cellular architecture of the leaves of *Chlorosphagnum* compared to those of extant Sphagnales may provide a first glimpse of another extinct lineage of Sphagnopsida next to the Palaeozoic Protosphagnales. Recent analyses based on estimated rates of molecular evolution suggest that Sphagnopsida as a whole may have diverged from other mosses in the beginning of the Carboniferous, ca. 350 Ma (Harris et al. 2022). Modern *Sphagnum sensu stricto*, by contrast, has been considered to have diversified much more recently, with the most recent common ancestor of almost all extant peat mosses having emerged 7–20 Ma (Shaw et al. 2010), coincident with the late Miocene and Pliocene expansion of boreal and arctic ecosystems at high latitudes (Taggart and Cross 2009, Shaw et al. 2010). More recent finds, however, document that *Sphagnum sensu stricto* was in existence already by the Eocene (Frahm 2009, Riegel and Wilde 2016), and also the divergence of the species-poor, largely Southern-Hemisphere lineages of Sphagnales – with *Ambuchanania*, *Eosphagnum*, and *Flatbergium* comprising taxa with rather exotic features like *Chlorosphagnum* – may be significantly more ancient (34–102 Ma, Shaw et al. 2010). Most of the Mesozoic and Early Cenozoic would thus span a long period of potentially extensive extinction on the stem-group of *Sphagnum sensu stricto*.

The nematodontous lineage, to which *Polytrichastrum* belongs, is thought to have diverged from the arthrodontous lineage during the Early Permian (c. 290 Ma) (Harris et al. 2022); the oldest finds of polytrichopsid fossils in particular (*Talchirophyllites* CHANDRA) date back to the Permian (Ignatov and Maslova 2021), even though the oldest unequivocal Polytrichales are again Early Cretaceous in age (Bippus et al. 2017, 2018). Similarly, the Diphysciaceae probably diverged from the remaining arthrodontous mosses (except the Buxbaumiaceae) in the Early Triassic (c. 250 Ma) (Harris et al. 2022). Altogether, the presence of *Polytrichastrum* and *Polytrichum* (Konopka et al. 1997),

as well as *Physcidium*, in the Cretaceous is therefore not surprising.

The resolution of moss relationships in the analysis of Harris et al. (2022) remains ambiguous after the divergence between the Diphysciaceae and remaining arthrodontous mosses; in this respect, the diverse gametophyte fossil record assignable to the Leucobryaceae, represented here by *Campylopus*, *Dicranodontium* and the extinct genus *Canaliculidium* together with an additional new leucobryoid genus from the Lower Cretaceous of Vancouver Island (Bippus 2022), forms robust support for the phylogenetic inference that these are old lineages (Liu et al. 2019), which are possibly significantly older than the Cretaceous. Since the Ditrichaceae also belong in the Dicranales, the same is true for the spore capsule that is probably assignable to this family.

The Catefica palaeoenvironment

The Catefica mesofossil flora was extracted from sediments of the Almargem Formation, a sedimentary sequence thought to have been deposited by a system of braided rivers and channels (Rey 1993; see also Mendes et al. 2018b). The small plant fragments that comprise the Catefica mesofossil flora reflect plant remains washed into small depositional accumulations from the surrounding vegetation of disturbed and more stable sites on the floodplain, permanent and temporary ponds and lakes, and also from more elevated, drier, and perhaps more distant sites. Because transport of plant fragments in water may be gentle, the distance from where plants were growing to the final deposition of their fragmentary remains is difficult to establish, but many of the plant fossils preserved in the Catefica mesofossil flora, including the fossil mosses, are delicate. Together with the preservation as charcoal, which is exceptionally brittle, this indicates that the fossil mosses were probably not transported over long distances.

Most of the fossils in the Catefica mesofossil flora are flowers, fruits, seeds, stamens and other remains of angiosperms. Chloranthoid angiosperms are particularly common and diverse, and comprise approximately 40 % of all angiosperm specimens and about 28 % of all angiosperm species (Friis et al. 2022, 2023), Magnoliid angiosperms, including forms referable to Canellales, Laurales and Piperales, account for about 30 % of all specimens. Only 3–4 % of angiosperm specimens can be assigned confidently to eudicot angiosperms. Based on knowledge of early angiosperms from other Early Cretaceous localities (e.g., Mohr et al. 2008, Coiffard et al. 2013, Friis et al. 2011, 2018, 2019a, 2022, Jud 2015), as well as in analogy with the habits of extant Chloranthaceae and Piperales, many of these angiosperms were probably of small stature and some were probably water plants related to extant Nymphaeales.

Non-angiosperm seed plants are also well-represented at Catefica, and conifer pollen is especially prominent in the dispersed palynoflora of the Almargem Formation (Mendes et al. 2018b). The importance of conifers in the floodplain

vegetation, most likely on slightly drier sites, is further supported by the presence in the Catefica mesofossil flora of vegetative axes, seeds and pollen cones of several kinds of conifers, likely including relatives of extant Araucariaceae (*Callialastrobus sousai* J.KVAČEK et M.M.MENDES, Kvaček and Mendes 2020) and Podocarpaceae (*Friisia lusitanica* M.M.MENDES et J.KVAČEK, Mendes and Kvaček 2020), as well as extinct Cheirolepidiaceae (*Watsoniocladius cunhae* J.KVAČEK et M.M.MENDES, Kvaček and Mendes 2021).

Similarly prominent in the Catefica mesofossil flora are seven formally described species of chlamydospermous seeds assigned to the informal Bennettitales-Erdtmanithecales-Gnetales (BEG) group, as well as several other seeds of this group which are not yet formally described (Mendes et al. 2020, Friis et al. 2022). As with angiosperms, based on knowledge from other Early Cretaceous localities (Crane and Upchurch 1987, Friis et al. 2011), as well as analogy with some species of extant *Ephedra*, many of these BEG seeds were probably produced by plants of small stature and weedy habit that colonized ephemeral open habitats in high-energy parts of the flood plain (Friis et al. 2019a, b).

Spore-bearing plants are represented in the Catefica mesofossil flora by fragments of fern leaves, sporangia, clusters of anemiaceous microspores, as well as megaspores of marsileaceous, selaginellaceous and isoetaceous affinity (see Friis et al. 2019a). Fern spores are also prominent in the dispersed palynoflora with schizaealean taxa, which today are often plants of open, somewhat dry habitats, especially well represented (e.g., *Costatoperforosporites friisiae* M.M.MENDES, E.BARRÓN, BATTEN et PAIS, Mendes et al. 2017). Scattered remains of the extinct fern genus *Onychiopsis* M.YOKOYAMA, with clear xeromorphic adaptations also signal water-stressed conditions, perhaps a result of saline influences (Friis and Pedersen 1990). Other ferns, related to extant Marsileaceae (e.g., *Molaspora* sp., *Arcellites punctatus* E.M.FRIIS, K.R.PEDERSEN et MARONE, Friis et al. 2014b), are more conclusively plants of wet or fully aquatic habitats.

Against this background, moss remains form an only minor component of the Catefica mesofossil flora but help to complete the picture of the vegetation from which the assemblage of plant fragments at Catefica was derived. Mosses are most common in sample Catefica 49 collected at the base of the outcrop in a silty horizon intercalated in a sequence of mainly cross-bedded sands, suggesting an unstable floodplain with active erosion, consistent with the inference that there were open habitats not always crowded out by vascular plants. Some broad environmental conclusions are also possible based on the ecological preferences of their nearest living relatives, supplemented in some cases by Ellenberg indicator values for light, moisture, reactivity (pH) and nitrogen availability (as measure of fertility) where they are available for relevant extant species (e.g., van Zuijlen et al. 2023; data at DOI: 10.16904/envidat.348).

Extant Sphagnopsida flourish in cool to cold temperature conditions in wet, partly anoxic environments where they are

often important in the formation of peatlands (Crum 1988). While *Chlorosphagnum* differed in leaf morphology from the extant *Sphagnum*, the combination of chlorophyll and hyaline cells suggests broadly similar habitat preferences and Ellenberg indicator values for 37–38 (depending on environmental variable) *Sphagnum* species in Europe clearly show their preference for high light, moist to wet conditions, and acid to extremely acid infertile sites (van Zuijlen et al. 2023).

Extant *Polytrichastrum* and extant Diphysciaceae occupy a wider range of habitats. Diphysciaceae grow both in forests and in open terrain, as well as on rotten wood, rocks, or soil, in fully or partly shaded places in moist, wet or even submerged habitats (Magombo 2003). Some species can also grow in more exposed habitats, but then at high elevations or in the Arctic, suggesting cool or cold conditions. *Polytrichastrum* grows in environments that range from dry somewhat shaded environments to moist or wet places, usually on siliceous soils, as well as rock crevices (e.g., Nyholm 1969). Similarly, available Ellenberg indicator values for 8–9 species of *Polytrichum* and *Polytrichastrum* in Europe indicate conditions ranging from semi-shade to high light, usually moist to wet conditions on acid to moderately acid, infertile to somewhat fertile sites (van Zuijlen et al. 2023). The tolerance of *Polytrichastrum* for low nutrient conditions is further emphasized by *Polytrichastrum sexangulare*, which grows in late snow beds (Nyholm 1969) and has Ellenberg indicator values indicating its preference for acid and extremely infertile sites (van Zuijlen et al. 2023).

Dicranodontium is distributed in the Holarctic as well as in subtropical and tropical mountains (Frahm 1997, Frey and Stech 2009, Bonfim Santos and Stech 2017) where extant species grow on siliceous rocks, rotten wood, soil, peat, and tree bark, mostly in cool and humid habitats (Frahm 1997). Ellenberg indicator values for the habitats of the three species of *Dicranodontium* in Europe indicate their preference for semi-shade on moist, acid and infertile soils (van Zuijlen et al. 2023).

Extant species of the large genus *Campylopus* (c. 150 species) occur in a wide range of habitats, mainly in cool-temperate regions (Frahm 1990, Bonfim Santos and Stech 2017). Many species grow in habitats affected by natural or human-induced disturbance (L. H., personal observation) as also suggested by available Ellenberg indicator values for the habitats of the 17 species of *Campylopus* in Europe (van Zuijlen et al. 2023). These indicate their preference for sites with semi-shade to fully open conditions, that are acid, nutrient-poor, and with the exception of *Campylopus introflexus* (HEDW.) BRID., *C. oerstedianus* (MÜLL. HAL.) MITT., and *C. pilifer* BRID., relatively moist or wet.

Taken together, the paleoenvironmental indications based on the extant relatives of the assemblage of fossil mosses in the Catefica mesofossil assemblage suggest that they grew in wet to moist environments of low pH and overall poor nutrient status. The remarkably broad taxonomic diversity

coupled with a relatively low abundance of moss remains in the mesofossil flora indicates that mosses – albeit rarely preserved – occurred widespread across different habitats in the local environment. However, they appear not to have been a significant part of the floodplain vegetation in terms of biomass.

Conclusions

The abundance, diversity and excellent preservation of the fossil mosses from the Catefica mesofossil flora adds significantly to the fossil record of mosses from the later Mesozoic. The fossils are three-dimensionally preserved, generally with excellent morphological and anatomical details, and present an interesting mix of taxa, including some modern-looking species of widespread genera alongside more unexpected occurrences of exotic taxa, and still others with combinations of features unknown in modern mosses. However, it is striking that all seven types recognized can be assigned reliably to extant orders. Four, *Chlorosphagnum cateficense*, *Physcidium tortuosum*, *Physcidium simsimiae* and *Canaliculidium fissuratum*, are sufficiently distinct to warrant the creation of new genera. Three, *Polytrichastrum incurvum*, *Dicranodontium minutum* and *Campylopus lusitanicus*, are readily assignable to extant genera, but none correspond fully to any extant species. Recognition of Sphagnales, Polytrichales and Dicranales adds to previous evidence of the presence of these orders during the Cretaceous and indicates that they were geographically widespread at that time. Recognition of Diphysciales from the Early Cretaceous provides the first robust evidence of this group in the Mesozoic. *Chlorosphagnum* exhibits leaf architecture distinct from that of the extant genera, and also from the doubtfully related Protosphagnales, which is known from the Palaeozoic and earlier Mesozoic. It therefore provides important new data on the fossil history of a key group of mosses.

Based on the ecological preferences of their nearest living relatives and consistent with other discoveries of fossil mosses from the Cretaceous of North America the mosses preserved in the Catefica mesofossil flora likely grew in more-or-less open conditions, perhaps as colonisers of bare substrate in disturbed, and moist or partly wet areas, with *Chlorosphagnum*, and possibly *Physcidium*, growing in the wettest sites. The ecological tolerances of the nearest living relatives of the fossil mosses also suggest that they grew in areas that were primarily of low pH and low nutrient status.

The fossil specimens recovered from the Catefica mesofossil flora are also consistent with previous record of mosses in the Cretaceous in that they all belong to lineages of mosses (Sphagnales, Polytrichales, Diphysciales, Dicranales) that diverged prior to the origin of the Bryidae (Liu et al. 2019). Only the records of the Tricostaceae from the Apple Bay locality stand out (Shelton et al. 2015, 2016, Tomescu 2016). This contrasts markedly to the assemblage of mosses recorded from Myanmar amber, which is thought

to be of Cenomanian age (e.g., Shi et al. 2012), within which many of the moss fossils are assignable to lineages that appear to diverge later, such as Hypnodendrales (Hedenäs et al. 2014), based on current models of moss phylogeny. This potential mismatch is worthy of a closer examination, including through dated phylogenies based on DNA data, because it is of central importance in discussions of fossil evidence for the age of the Bryidae, including the Hypnanae, the most diverse lineage of mosses today.

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