Acta Geologica Polonica, Vol. 75 (2025), No. 4, e64
DOI: 10.24425/agp.2025.157029

Rhizome and leaf anatomy of *Rhizocaulon huberi* H.-J. Gregor (Cyperaceae, Miocene) and nomenclature of the genus *Rhizocaulon* Saporta ex Schimp. et Schenk

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ABSTRACT:

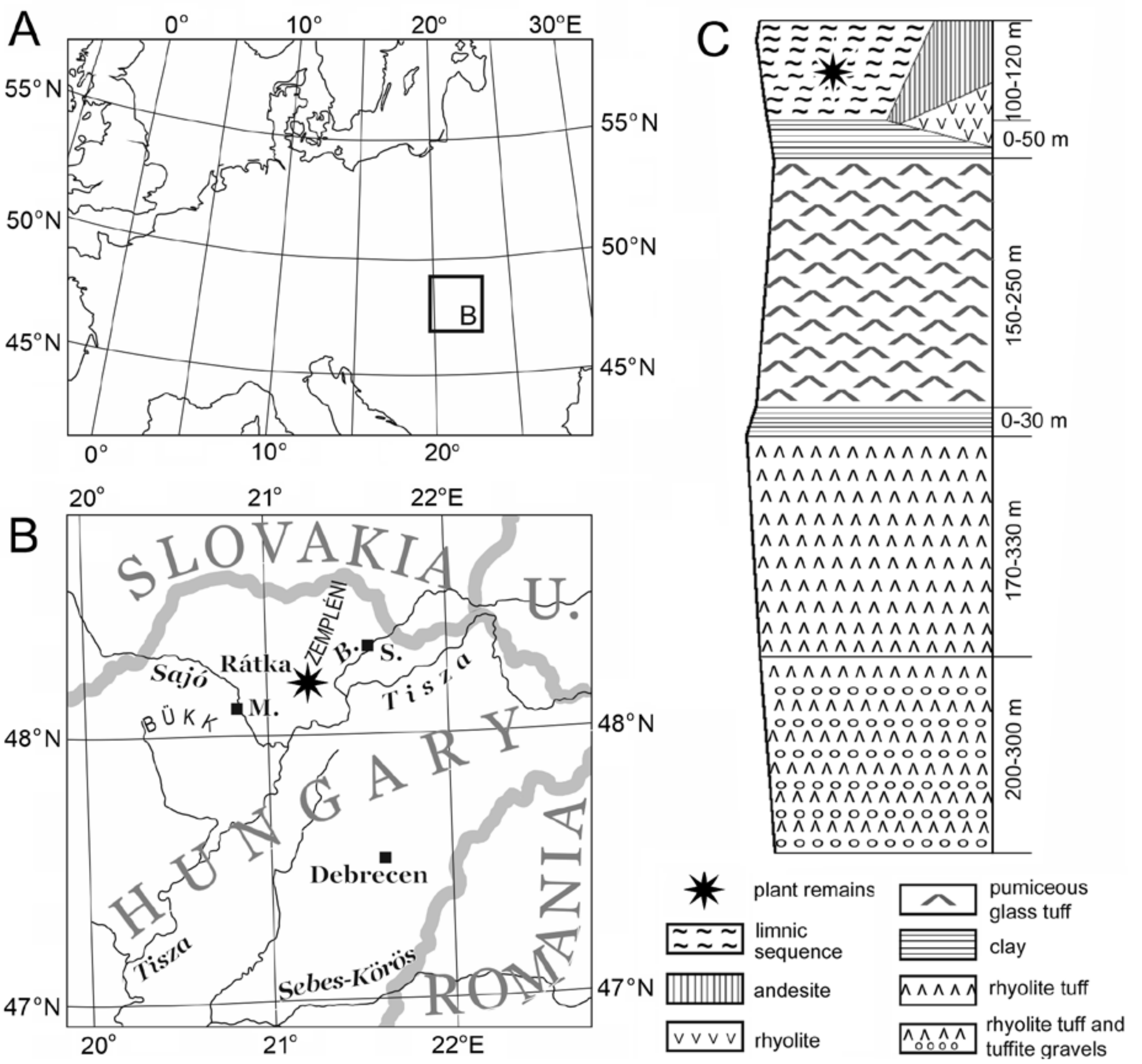
Halamski, A.T., Kraski, J., Erdei, B. and Durska, E. 2025. Rhizome and leaf anatomy of *Rhizocaulon huberi* H.-J. Gregor (Cyperaceae, Miocene) and nomenclature of the genus *Rhizocaulon* Saporta ex Schimp. et Schenk. *Acta Geologica Polonica*, **75** (4), e64.

Rhizocaulon huberi H.-J. Gregor is redescribed based on new specimens from the type locality of Rátka (Miocene, Hungary). The material consists of rhizomes, roots, and leaves in physical connection. The roots branch from the rhizome from all sides and their primary cortex has radial strands of tissue separated by lacunae of schizogenic origin or resulting from tangential lysigeny. Tristichously arranged leaves that form a pseudostem are dorsiventral with internal aerenchyma. The type material of *R. huberi* is most probably heterogeneous (it contains septate rhizomes with roots branching in whorls which do not belong to the same plant). Poaceous affinities proposed formerly for *R. huberi* can be ruled out on account of phyllotaxis. *Rhizocaulon huberi* is probably a representative of the Cyperaceae (with similarities to *Diplasia* Rich.), although this conclusion should not be uncritically extended to the other representatives of this fossil-genus. The first valid publication of the genus *Rhizocaulon* was in 1885, so it should be cited as *Rhizocaulon* Saporta ex Schimp. et Schenk. *Rhizocaulon brongniartii* from the Oligocene of southern France is selected herein as the type species, which allows the preservation of the current understanding of *Rhizocaulon* as a fossil-genus for permineralised rhizomes of monocotyledons. Andrews' (1955) choice of the Cretaceous species *R. macrophyllum* as the type of *Rhizocaulon* is based on an illegitimate name and is thus null and void.

Key words: Plant anatomy; Silicification; Botanical nomenclature; Angiosperms; Monocot; Fossil; Sarmatian.

INTRODUCTION

The present contribution has resulted from a re-study of Miocene plant fossils first reported and described from Rátka in Hungary by Huber and Pavlicek (2008) and Gregor (2008). Re-sampling of the type locality of *Rhizocaulon huberi* H.-J. Gregor allowed the making of microscopic preparations and thus a more detailed anatomical study. Thanks to this, the previously presented reconstruction of the whole plant is corrected and the systematic affinities of the described species are elucidated.



Text-fig. 1. Geographic and geologic context of the studied material. A – Map of Central Europe with the inlet showing the extent of the more detailed map. B – Map of north-eastern Hungary: MOUNTAINS in capitals, *rivers* in italics, towns in Roman typeface. The studied locality is denoted by an asterisk. *B.* – Bodrog; M. – Miskolc; S. – Sárospatak. C – A generalized lithostratigraphic section of the Rátka area (modified after Gyarmati *et al.* 1977) with the position of the plant-bearing strata.

During the preparation of the formal description of the material described in this study, it became clear that the use of the generic name *Rhizocaulon* was far from straightforward. This is why the present authors felt it necessary to include a section dealing with botanical nomenclature. However, it should be stressed that this section is limited to study of the formal aspect of the introduction of the genus *Rhizocaulon* and to the selection of the type species. Palaeobotanical study of the material from southern France, on which the genus is based, is out of the scope of the present study.

GEOLOGY

The locality at Rátka (or Rátka–Hercegköves-hegy, that is, Hercegköves hill) (48º12’32”N 21º15’40”E), misspelled as Ratká in many earlier accounts, is located in north-eastern Hungary, in the southern part of the Zempléni Mountains (also referred to as the Tokaj Mountains), in a triangle defined by the towns of Rátka, Szerencs, and Mád (Text-fig. 1A, B). The Tokaj-Slanské Vrchy mountain chain, including its southern (Hungarian) and northern (Slovakian) parts, occupies the north-eastern part of the Carpathian-

Pannonian Region close to the Carpathian Orogenic belt (Kováč *et al.* 2007). Coupled with its complex tectonic evolution (connected to the underlying microplates, ALCAPA and Tisza-Dacia), widespread volcanic activity characterised the Carpathian-Pannonian Region from the Miocene onward (Csontos *et al.* 1992; Szabó *et al.* 1992; Harangi 2001; Karátson *et al.* 2022, 2025; Lukács *et al.* 2024). As a result, the Tokaj Mountains are dominated by andesitic and rhyolitic volcanics with a series of north-south trending volcanic complexes (Gyarmati 1977; Zelenka *et al.* 2012). Palaeovolcanic research suggested initial shallow marine, later subaerial conditions of the eruptions and proposed probable locations of calderas (Gyarmati 1977; Kováč *et al.* 2007; Zelenka *et al.* 2012). Four silicic explosive volcanoclastic units have been distinguished in the Tokaj Mountains (Lukács *et al.* 2024, fig. 1b): the oldest, Sátoraljaújhely Unit in the eastern part, Hegyköz Unit in the northern part, and the youngest, Vizsoly Unit in the western part. The silicic pyroclastic rocks of the southern part of the Tokaj Mountains have been described as a fourth unit, the Szerencs succession or Szerencs Unit (Zelenka 1964; Lukács *et al.* 2024). This unit has been assumed to comprise volcanoclastic deposits 200–350 m thick, with intercalations of redeposited tuff, tuffite, argillaceous sediments, and occasionally rhyolitic and andesitic lavas suggesting several, but hardly separable eruption subunits (Zelenka 1964; Lukács *et al.* 2024).

Previously published K-Ar datings for the Tokaj Mountains postulated silicic explosive volcanism lasting from 15.2 Ma to 11.2 Ma (Pécskay *et al.* 1986, 2006; Zelenka *et al.* 2012). Earlier interpreted K-Ar ages for the Szerencs Unit yielded 12.2 ± 0.5 to 11.3 ±0.5 Ma (Pécskay and Molnár 2002). Updating these ages, zircon U-Pb dates indicate volcanism starting later and extending over a shorter time span, between 13.1 and 11.6 Ma (Lukács *et al.* 2024). According to Lukács *et al.* (2024), volcanism in the Tokaj Mountains started with the Sátoraljaújhely eruption (13.1 Ma), which together with the Szerencs eruption (c. 12 Ma) are suggested to have been large and caldera forming eruptions. A younger volcanism in the Tokaj Mountains may also be supported by Karátson *et al.* (2025) identifying the Dobi ignimbrite (c. 13 Ma; resulting from a large magnitude eruption from a source area south of the Tokaj Mountains) among the oldest volcanic products (Sátoraljaújhely Unit) of the Tokaj Mountains.

The limnic sequence at Rátka (Rátka–Hercegköveshegy; Szerencs Rhyolite Lapilli Tuff Formation, Erdőbénye Member; Babinszki *et al.* 2024), which has yielded silicified remains of plants including those studied herein, overlies the various volcanic products of the Szerencs Unit, dated to c. 12 Ma (Text-fig. 1C; Huber and Pavlicek 2008, fig. 6). Fossilisation took place by means of hydrothermal systems coupled with the volcanic activity of the area. Studies of hydrothermal products indicated that hydrothermal activity in the Mád-Szerencs Hills region (including Rátka) was multiple and extended, most probably related to various eruptions. K-Ar dates available for the hydrothermal systems in this region vary between 12.1 and 10.4 Ma (Pécskay and Molnár 2002), extending their formation to as late as the Pannonian. In summary, lithostratigraphic and radiometric data suggest that the limnic sequences yielding the silicified plant fragments of Rátka are most probably (not older than) Sarmatian (a regional stage of the Miocene, corresponding to the middle and upper part of the Serravallian, which is in turn the upper part of the Middle Miocene; Rasser *et al.* 2008).

MATERIAL AND METHODS

The abandoned quarry at Rátka was re-sampled in 2018. Its state during the fieldwork did not show any significant differences compared to the description of this locality (including photographs) given by Huber and Pavlicek (2008). More than fifty silicified fossil specimens were collected, ranging in size from about 1 cm to about 11 cm, most of which were identified as *Rhizocaulon huberi*. These specimens were either isolated plant fragments (rhizome and leaf pieces; Pl. 1) or blocks of siliceous rock that, if cut and polished (Pls 2, 5), allowed observation of the anatomical structures of the plants. Specimens were extracted from the superficial weathered layer of the plant-bearing rock, from two shallow pits existing in the quarry (most probably resulting from the activity of fossil collectors). The work is partly based on an unpublished M.Sc. thesis by JK at the Faculty of Geology of the University of Warsaw under the supervision of ED (Kraski 2024).

Grinding and microscopic preparations were done in the laboratory of the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw. Out of the collected material, more than forty selected specimens were cut and the obtained surfaces (mostly transverse sections, two longitudinal sections) were polished using SiO_2-based grinding powders, mostly 400 (9 µm grain size) and 1000 (3 µm grain size). Moreover, 24 microscopic preparations were made. Selected specimens were immersed in a resin (Araldite 2020 or Epidian), cut into slices at least 5 mm thick, polished, glued into microscope slides, milled until about 70–100 µm thick using Petrothin, and finally polished on a glass using 1000 grinding powder. The final microscopic preparations are 40–60 µm thick (Kraski 2024, pp. 14, 15).

Photographs of the rhizome (Pl. 1, Figs 1, 2) were made using a Canon 350D camera with a Canon EF 100 mm macro lens, under two oblique lights (main, from top left; accessory, bottom right). Other photographs were made with a Keyence VHX-7000 digital microscope at the Faculty of Geology, University of Warsaw. Images were digitally edited with Adobe Photoshop software.

The type material of the investigated species is deposited in the Naturmuseum Augsburg (NMA). The new material studied and illustrated here is deposited in the collections of the S. J. Thugutt Geological Museum, Faculty of Geology, University of Warsaw (MWGUW) under collection number ZI/119. Individual specimens (rock pieces or microscopic slides) are cited as MWGUW ZI/119/1, 119/2, and so on. If several specimens are glued to the same microscopic slide, they are referred as 119/7A, 7B, and so on.

The silicification of the investigated material was not under detailed study. It is, however, of importance for the following descriptions to note that the silicification was neither perfect nor uniform. Generally speaking, the external parts of the studied plant fragments were preserved better than the internal ones on the one hand, and the leaves than the rhizome on the other hand. In the leaves in some cases cellular preservation allows study of the anatomy of vascular bundles (Pl. 16), but the epidermis is preserved as a layer without observable cellular structures (Pl. 15). In the analysed polished sections and microscopic preparations, the interior of the rhizome consists of a mass of amorphous silica; it is unclear if this corresponds to a hollow existing *in vivo* or if it results from *post mortem* decay. In any case, the preservation of the vascular bundles in the rhizome (Pl. 7) is poorer than that of those in the leaves (Pl. 16). Finally, some specimens are preserved better than the others.

The International Code of Nomenclature for algae, fungi, and plants has been followed (Editorial Committee of the Madrid Code 2025), including abbreviations of authors' names following Brummitt and Powell (1992).

SYSTEMATICS

Division Angiospermae Braun et Doell ex Doell
Class Monocotyledoneae DC.
Order and family *incertae sedis*

Genus *Rhizocaulon* Saporta ex Schimp. et Schenk

1861. *Rhizocaulon* Saporta; Heer, p. 135 [nom. illeg.];
1862. *Rhizocaulon* Saporta, p. 197 [nom. illeg.];
1870. *Rhizocaulon* Saporta ex Schimp.; Schimper, p. 418 [nom. illeg.];
1885. *Rhizocaulon* Saporta ex Schimp. et Schenk; Schimper and Schenk, p. 390.

TYPE SPECIES: *Rhizocaulon brongniartii* Saporta ex Schimp. et Schenk; Saint-Zacharie, Provence, France; Cainozoic (Oligocene?); selected herein (see below, nomenclatural section).

Rhizocaulon huberi H.-J. Gregor

(Text-fig. 2, Pls 1–17)

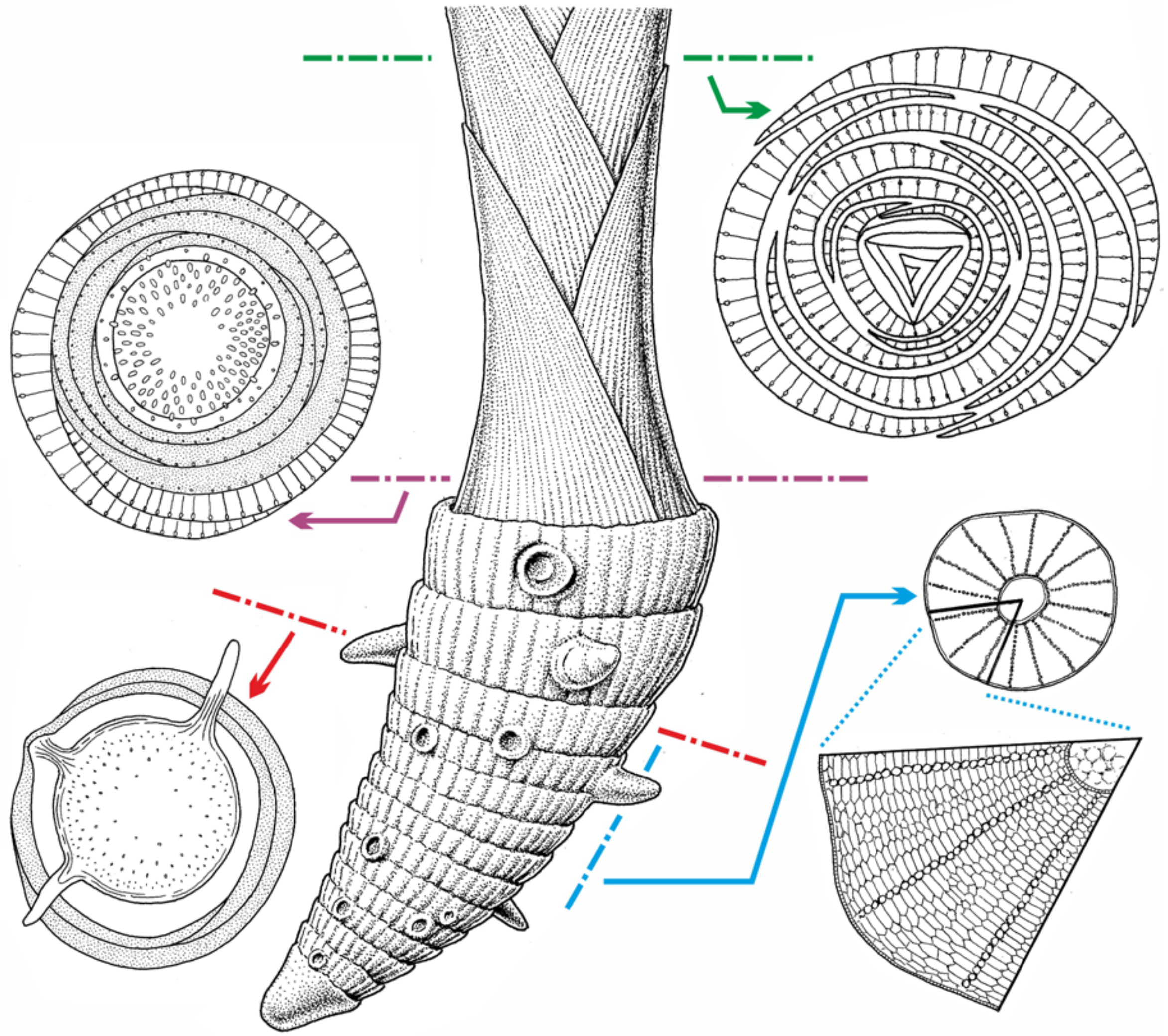
v*p 2008. *Rhizocaulon huberi* nov. spec.; Gregor, p. 23, fig. 1A–D, G–I, K–M; pls 1–3; pl. 4, figs 1, 2, 5, 8; pl. 5; pl. 6, figs 1–3; pl. 7, figs 1–6; pls 8–10; non fig. 1E, F, J; pl. 4, figs 3, 6; pl. 6, fig. 4, 5.
p 2008. *Rhizocaulon huberi*; Huber and Pavlicek, p. 16; fig. 16; non figs 10–12, 17.

TYPE MATERIAL: Holotype NMA 2006-57/1796 ≡ NMA 2006-58/1796 ≡ NMA 2006-74/1796, a rhizome fragment c. 58 mm long, c. 17 mm thick at the thicker end, c. 9 mm thick at the thinner end. The triple number of the single specimen designated as the holotype of *Rhizocaulon huberi* is due to a *lapsus calami*. The same specimen was given the number 2006-58 in the text (Gregor 2008, p. 24), 2006-57 in the legend of plate 1 (Gregor 2008, pl. 1, figs 1, 2, 4), and 2006-74 in the legend of plate 3 (Gregor 2008, pl. 3, fig. 1).

The rest of the collection described in the protologue is designated as 'isotypes' (Gregor 2008, p. 24). As currently understood, this notion should be used for Recent plants only, given that the time averaging in a fossil sample precludes treating a collection of fossils as a 'single gathering' in the sense of the ICN (see e.g., Gravendyck *et al.* 2021). The referred specimens should thus be considered as paratypes. Moreover, the type material is interpreted here as heterogeneous (see below).

MATERIAL: Over fifty individual fragments (of rhizomes, roots, and leaves; see details below) of various sizes, including over forty sectioned and polished pieces, as well as 24 microscopic preparations made on their bases.

EMENDED DIAGNOSIS: Rhizomes somewhat elongated (up to at least 8 cm long), usually 1–2 cm



Text-fig. 2. *Rhizocaulon huberi* H.-J. Gregor, partial reconstruction of plant, showing rhizome with roots connected to pseudostem formed by leaves in tristichous arrangement. Four transverse sections shown: through pseudostem (green, top right), rhizome (red, bottom left), intermediate zone between pseudostem and rhizome (violet, top left) and root (blue, bottom right, schematic, with a section shown in detail below). Spikes or spikelets not shown due to lack of attachment. Not to scale. Drawing by B. Waksmundzki.

in diameter, of typical monocotyledonous anatomy; roots branching from all sides, at an approximately right angle to the rhizome. Leaves tristichously arranged, forming a pseudostem, dorsiventral, most of the interior occupied by air chambers.

DESCRIPTION: The material studied in the present contribution consists of permineralised plant fragments, and namely: rhizomes, roots, and leaves forming pseudostems; physical continuity between fragments belonging to each of these categories can be established, so their belonging to a single biological species *R. huberi* is under no doubt. On the other hand, hollow axes with transverse septa (Gregor 2008, pl. 6, fig. 4) and spikes (Pl. 17) have not been found in physical continuity with the above-mentioned fragments; their relationship to the discussed biological species is conjectural.

Rhizome, external morphology. General form irregularly cylindrical, longer than wide (Pl. 1, Figs 1–2; Pl. 5). The longest preserved fragment (NMA 2006-67/1796; Gregor 2008, pl. 1, figs 6–8) is c. 8 cm long. Nodes with basal parts of cataphylls preserved (Pl. 1, Figs 1–3, green arrows). Internodes rather short, 2–7 mm, usually about 5 mm long. Roots arise from the rhizome irregularly from all sides, at right angles, with smaller roots being sometimes up to 6 per cm^2.

Rhizome, anatomy. Rhizome subcircular in cross-section (Pl. 2, Figs 1–4), typically 1–2 cm in diameter, maximum recorded diameter about 3 cm. In transverse section the rhizome appears as constituted by a central mass of amorphous silica, occupying about 2/7 of the total diameter, corresponding to either an original cavity or a parenchymatous tissue that has not been fossilised (generally speaking, the preservation of the external layers of the rhizomes is better than that of the internal layers). This siliceous mass is surrounded successively by layers interpreted as a parenchyma, vascular bundles, an endodermis, an inner cortex, a median cortex, a hypodermis (or outer cortex), and an epidermis (rhizodermis). In turn, the entire rhizome is surrounded by leaf sheaths.

The interpretation of the centrally located siliceous mass as remains of a parenchymatous pith is favoured, insofar as parenchyma cells seem to be preserved in certain specimens (Pl. 3; Pl. 4, Fig. 1). It is surrounded by a layer of tissue where cellular details are not preserved, except for the numerous, irregularly distributed vascular bundles (Pl. 3; Pl. 4 Fig. 1; Pl. 6). It occupies 3/7 of the total diameter of the rhizome. The density of vascular bundles ranges from 5 to 14 per mm^2 (often about 8 per mm^2), with individual bundles, about 50–100 μm in diameter, increasing in density towards the exterior of the rhizome. Inside the vascular bundles darker, oval structures are present. They probably represent the phloem and xylem (Pl. 7, Fig. 2), constituting collateral vascular bundles. In the outer regions of the vascular bundles, rounded cells are visible, possibly representing fibres (Pl. 7, Fig. 2). The stele (central cylinder) is limited externally by a dark layer with no visible cellular structure, representing the endodermis. The derivatives of the endodermis constitute the median cortex (mc in Pl. 7, Figs 1, 2).

Externally to the inner cortex there is a layer of the primary median cortex, occupying 2/7 of the total rhizome diameter (mc in Pl. 7). The cellular structure of the layer is not preserved (possible formed by aerenchyma), the only visible structures being individual, randomly distributed single cortical vascular bundles, resembling those found within the stele, only much less densely spaced (Pl. 7). Externally, a 100–200 μm thick layer of small, rounded, thin-walled cells is visible, representing the hypodermis or outer cortex (h in Pl. 7, Figs 1, 2). The outermost layer of the rhizome is the epidermis (or rhizodermis; r in Pl. 7). Although its cells are not preserved in the examined material, the original presence of an epidermis is indicated by a dark layer (Pl. 7, Fig. 2).

In several cross-sections, roots originating within the stele and emerging perpendicularly from the rhizome can be seen (Pl. 3; Pl. 4, Figs 1–2; Pl. 11). In one of the available longitudinal sections of the rhizome several densely spaced, thin, subparallel, acroscopically oriented structures emerge from the outermost layer of the rhizome. These are probably the cataphylls observed in external view (Pl. 5). In transverse section they appear sometimes as crescentic structures similar in shape to euphylls (Pl. 3).

Root, external morphology. Externally, roots are elongated, the longest fragment available is about 40 mm long. A conical root cap was observed in external view (Pl. 1, Fig. 3, red arrow). An emerging root with a root cap is also visible in the cross-section of the rhizome shown in Pl. 10.

Root, anatomy. The roots are circular in cross-section, about 1–3 mm in diameter, and are constituted (from the middle towards the exterior) by the stele, the cortex, and the rhizodermis (Pl. 8).

The root stele has a thickness accounting for about 1/5 of the root diameter. It consists of usually poorly preserved small, rounded parenchyma cells or fibres and several large, about 50 μm in diameter, metaxylem elements from xylem embedded within the former. The xylem is arranged in a ring (Pl. 9, Fig. 2). The outermost part of the stele is bounded by the endodermis, which appears as a 10–20 μm thick layer of elongated, rectangular, thick-walled cells (Pl. 9, Fig. 2).

Externally from the inner cortex, a layer of the median cortex is located. It accounts for about 4/5 of the root diameter and is composed of parenchymatous tissue. The layer shows a star-shaped structure: a dozen or so radial strands, each formed by a single row of round parenchyma cells (Pl. 8, Fig. 2; Pl. 9, Fig. 1), are separated by sections of altered parenchyma exhibiting a system of remnants of cells interspersed with lysigenous intercellular lacunae (Pl. 8, Fig. 2; Pl. 9, Figs 1, 4). These features are consistent with tangential lysigeny model proposed by Jung *et al.* (2008) or schizogeny. The outermost layer of the root is formed by the rhizodermis, consisting of a single layer of approximately square-shaped cells in cross section, measuring about 10 μm (Pl. 9, Fig. 3).

In some cross-sections, longitudinal structures starting in the stele and perpendicular to it, are visible (Pl. 8, Fig. 3, top left). They probably represent lateral roots.

Leaf, external morphology. The leaf lamina is linear with parallel-sided margins, 10–22 mm wide, and the largest collected fragment is about 54 mm long. Leaves are preserved either flat, with a longitudinal bend in the median part (thus V-shaped in transverse section) or with both halves superimposed on each other (Pl. 1, Figs 6, 7). Both surfaces show dense parallel ribbing (Pl. 1, Figs 4–7), thicker ribs about 2 per 1 mm. Between each pair of primary (thicker) ribs are 3–6 weaker ribs. The thicker ribs are spaced approximately 0.5 mm apart and correspond to the transverse septa between air chambers (see detailed description below).

Leaf, general arrangement. Tristichous phyllotaxis of the leaves is clearly observable (Pl. 11, Figs 1, 3; Pl. 12, Fig. 1). Leaves form a pseudostem (Pls 10, 11) up to 4 cm in diameter.

In most cross-sections of the rhizome, surrounding leaves are visible. The leaves directly adjacent to the rhizome do not exhibit developed air chambers. The interior of the leaf is filled with parenchymatous tissue. Black, granular structures are also present being probably a diagenetic infilling of some of the parenchymatous cells (Pl. 6). The outermost leaves have a typical anatomy with aerenchymatous tissue, as described in detail below. The vascular bundle pattern (see details below) is similar in both inner and outer leaves surrounding the cortex.

Leaf, anatomy. Leaves are dorsiventral, with major vascular bundles and a row of sclerenchyma fibres present only on the abaxial side. The leaf blade thickness is up to 2 mm. General organisation of the leaf from the external surfaces towards the interior is as follows: very thin upper and lower epidermides, indicated by dark layers (ep and ed in Pl. 14), but no cells are preserved; abaxial and adaxial chlorenchymata (both quite thin); and a thick layer of aerenchyma located between them. Air chambers are about 30–40 in number per leaf (Pl. 12, Fig. 1; a precise value is difficult to give, as septa separating the chambers are not seldom incomplete). There is no midrib.

The abaxial parenchyma (chlorenchyma) is c. 150 µm thick. The cells are rounded, closely packed, and have a diameter of 20–30 µm. A row of main vascular bundles (Pls 11–14) runs within the parenchyma layer, each embedded in the upper portion of each septum between two adjacent air chambers. The interveinal distance is about 500 µm. The vascular bundles are collateral and occur in two distinct sizes and are arranged alternately, with larger (200 µm long and 100 µm wide; vbm in Pl. 14) and smaller (50 µm long and 30 µm wide; vbn in Pl. 14) bundles appearing in succession. Two sheaths can be seen surrounding the vascular bundle (the outer or parenchyma sheath and the inner sheath or mestome; ms and ps in Pl. 16, Fig. 3). The gap observed facing the lower side refers to the phloem, following adaxially to the metaxylem, protoxylem, and the fibre cap (Pl. 16, Fig. 2). An adaxial sclerenchyma girder, crescentic in shape, is present in each bundle (sg in Pl. 16, Fig. 3).

In the adaxial chlorenchyma, a row of regularly spaced (50–100 µm apart) rounded dark structures 20–30 µm in diameter (vbs in Pls 14, 16) is visible. Usually there is a single such structure above each vascular bundle and 3–4 of them between each pair of adjacent vascular bundles. They likely represent small vascular bundles.

The presence of an adaxial epidermis is represented by a dark layer (ed in Pl. 15, Fig. 1). The adaxial chlorenchyma (p in Pl. 15, Fig. 1) is much thinner than the abaxial one, about 20 µm thick, and contains no vascular bundles. The parenchymatous cells are arranged in only two layers, are slightly flattened, and measure about 20 µm in length and 10 µm in height. Internally to the adaxial epidermis, it is possible to observe a darker band that could possibly be a narrow layer of fibres (s in Pl. 15, Fig. 1).

Air chambers (ae in Pl. 16) occupy the central part of the leaf between the abaxial and the adaxial chlorenchyma zones, up to 9/10 of the leaf's total thickness. Chambers are subrectangular in cross-section, up to 700 µm wide, and up to 2000 µm high. They are separated by parenchymatous septa longitudinally (sp in Pls 14, 16). Sometimes diaphragms consisting of stellate cells are present subperpendicularly to the septa (di in Pls 14, 16).

In transverse section up to six rounded structures, arranged vertically in a row, are present in the parenchymatous septa (vbt in Pls 14, 16). Sometimes clusters of rounded cells are visible within them, occasionally surrounding a round empty space. They can represent either smaller vascular bundles, or fibres, or both, but their state of preservation does not allow secure identification.

The diaphragms forming tangential walls between air chambers appear as a reticulum. In a straight (tangential) view, stellate cells forming the diaphragm are visible. They usually have 5–6 extensions (Pls 15–16). In this case, the mesh openings appear triangular in shape. In more oblique sections, the mesh openings take a more quadrangular form or are irregular in shape. The meshes are up to 20 µm in diameter.

Spike. Three ovoid structures have been found trapped between the halves of a leaf that was folded in half (Pl. 17). These are not in organic connection with any other part of the described material. These structures are ovate in shape, about 4.5 mm long and

2 mm wide, their surface showing low protuberances. Each has an estimated total of about thirty (only one side of the structure can be seen). These structures are interpreted as spikes or spikelets, although their biological relationship to the leaf taphonomically enclosing them is conjectural. The best-preserved spike is connected to a stalk about 11 mm long and about 0.9 mm thick. Two other presumed spikes lack apical parts and show a hollow interior.

REMARKS: In comparison with *R. huberi*, the type species *R. brongniartii* seems to differ in its having leaves with relatively smaller air chambers (Schumann 1893, pl. 28, fig. 10) and a stronger development of mechanical tissues (Schumann 1893, pl. 28, figs 6, 7). The Pliocene species *R. garzweilerense* H.-J. Gregor, Lieven et Winterscheid cannot be compared directly, as anatomical data are lacking; the size, however, is distinctly smaller (Gregor *et al.* 2010) than the *R. huberi* specimens described here.

In the investigated material there are two specimens requiring a separate comment. There are two fragmentary structures, a few centimetres long and about 1 cm in diameter, consisting of an external layer and a central axial structure separated by a hollow. They likely possess nodes and internodes. The nodes correspond to zones with numerous small root traces arranged in a whorl. These structures have been found neither in organic connection with the rhizomes or leaves, nor any of their counterparts could be observed in sections. They have been interpreted as lateral ramifications of the rhizome of *R. huberi* by Gregor (2008, fig. 1E). In the opinion of the present authors they do not belong to the same biological species as the rest of the material because of the differences in external morphology. Roots are randomly distributed in *R. huberi*, whereas these structures produce roots at distinct nodes. They also differ anatomically: according to the reconstruction by Gregor (2008), their vascular bundles are arranged in a ring, while in *R. huberi* they are more diffuse.

WHOLE PLANT RECONSTRUCTION

The authors of the present contribution have been in the fortunate situation of possessing fossil fragments showing physical connection between several plant organs and thus of proposing a supplemented and corrected reconstruction of the fossil plant *R. huberi* presented in the protologue (Gregor 2008).

The general organisation of the monocotyledonous plant from the Rátka locality (Text-fig. 2) can be summarised as consisting of a subterranean rhizome with roots and an aboveground pseudostem, arguably corresponding to a vegetative shoot. The orientation of the rhizome is a debatable issue. It was presented by Gregor (2008, fig. 1) as strongly curved, more horizontal than vertical. In the opinion of the present authors such a degree of curvature is excessive, insofar as the roots arise from the rhizome equally from all sides, whereas a nearly horizontal rhizome would possess more roots on its lower side. On the other hand, some rhizomes are distinctly curved (Pl. 1, Figs 1, 2), whereas others are more or less straight (Gregor 2008, pl. 1, fig. 7). As a consequence, the plant has been reconstructed as possessing a rhizome more or less vertical, even if sometimes curved (Text-fig. 2).

The presumed spikes might have been a part of this plant, but due to their lack of attachment or anatomical data, the present authors cannot assign them to the same species with certainty. Externally the rhizome appears to show nodes and internodes, even if this distinction has not been noticed in anatomical structures. The pseudostem is composed of leaves in tristichous arrangement. Four transverse sections are shown, showing the rhizome with roots, the rhizome-pseudostem intermediate region, the pseudostem, and a root.

The differences between the reconstruction presented above (Text-fig. 2) and that proposed by Gregor (2008, fig. 1) can be summarised as follows:

- the presumed lateral ramifications of the rhizome (Gregor 2008, fig. 1E, F) are interpreted here as belonging to another plant species, so not included in our reconstruction;
- the aboveground part of *R. huberi* is interpreted as a pseudostem formed by spirally arranged leaves, whereas transverse sections by Gregor (2008, fig. 1H, I) show a continuous external layer suggesting the existence of a stem;
- the uppermost transverse section by Gregor (2008, fig. 1J) does not seem to correspond to any structure observable in our material.

AFFINITIES OF THE STUDIED PLANTS

Rhizocaulon huberi was described in the protologue as belonging to the “Poaceae or Cyperaceae” (in that order; Gregor 2008, p. 23). The title of the paper by Gregor *et al.* (2010) on *R. garzweilerense* includes an apparently precise systematic assignment, “Eine neue Art von Cyperaceen-Rhizomen” [a new species of rhizomes of Cyperaceae], but in the text the affinities are described in a very different way:

"Ordo et fam. indet. (cf. Typhales, Poales, Cannales)" (p. 4), "systematische Zugehörigkeit bei Cyperaceen, Gramineen, u.a." [systematic position in Cyperaceae, Gramineae, and others] (p. 5).

The atactostelic anatomy of the rhizomes from the Rátka locality is clearly diagnostic of monocotyledonous angiosperms (de Candolle 1817; Doell 1857; Arber 1923). However, determination of the more precise affinities of the studied fossil plant within the natural system is an arduous task, insofar as rhizomes of monocotyledons show a high degree of similarity across various groups, and descriptions in neobotanical literature refer to specific positions of sections within mature organs, whereas such precision of location is often unobtainable in fossils (Erwin and Stockey 1991, p. 241). Moreover, the preservation of the studied material is not perfect and cellular details are frequently blurred, so several potentially diagnostic characters simply cannot be observed. However, due to the fortunate circumstance of physical connection of leaves with the rhizome having been preserved in some of the investigated specimens, additional characters can be taken into account.

The tristichous disposition of leaves is a relatively infrequent character among the monocotyledons and allows the present authors to immediately discard the families belonging to the Poales *s. s.* (the graminid group) having a distichous phyllotaxis (Kubitzki 1998a, p. 4; Kellogg, p. 122). Previously, the Gramineae Juss., nom. cons. [syn. Poaceae (R. Br.) Barnhart; de Jussieu 1789, p. 28; Brown 1814, p. 583; Barnhart 1895, p. 7] was suggested as one of two possible families for the Rátka material by Gregor (2008). Additionally, de Saporta (1862) suggested the Restionaceae R. Br. (Brown 1810, p. 243) as one of the families possible for *Rhizocaulon brongniartii* from Provence.

The tristichous phyllotaxis is characteristic of the Cyperaceae Juss. (de Jussieu 1789, p. 26; Dahlgren *et al.* 1985, p. 79), but by no means exclusive to that family. Other monocotyledonous families showing that character include the Juncaceae Juss. (de Jussieu 1789, p. 43; Balslev 1998, p. 252) and Pandanaceae R. Br. (Brown 1810, p. 340; Geesink *et al.* 1981, p. 7). Spiral phyllotaxis is present, for example, in the Alismataceae Ventenat (Ventenat 1799, p. 157; Haynes *et al.* 1998, p. 12) and in a certain number of commelinid families (Tomlinson 1969, p. 398). The Juncaceae possess true stems, and not pseudostems (Szynal and Mądalski 1931; Zimmermann and Tomlinson 1968; Cutler 1969; Balslev 1998), so this family can be ruled out for the Rátka plant with very high probability.

The general aspect of the studied plant is suggestive of the Cyperaceae on account of the pseudostem with a distinctly triangular inner shape (Pl. 11, Fig. 3). Such a structure, called also a false stem, is present in some species of *Carex* L. (Linnæus 1753, p. 972). It has been termed a pseudoculm by Reznicek and Catling (1986). Comparative data for Recent plants may often be of relatively little help, as the same structures are described under different names: for example, *Kobresia simpliciuscula* (Wahlenb.) Mack. (Wahlenberg 1803, p. 141; Mackenzie 1923, p. 349) is reported to have a 'false-stem' by Hedley (2014), but no such structure is mentioned in the descriptions of this species given either by Jermy *et al.* (2007, p. 188) or Stace (2019, p. 1021). Species of Cyperaceae reported to possess pseudostems include *Eleocharis dulcis* (Burm. f.) Trin. ex Hensch. (Burman 1768, p. 219; Henschel 1833, p. 186; Rajesh *et al.* 2021) and *Schoenoplectus juncoides* (Roxb.) Palla (Kunth 1837, p. 211; Palla 1888, p. 299; Umkhulzum *et al.* 2019). However, pseudostems occur also in the Musaceae Juss. (de Jussieu 1789, p. 61; Andersson 1998), Melanthiaceae Batsch nom. cons. (*Veratrum* L.; Linnæus 1753, p. 1044; Batsch 1802, p. 133; Troll 1954, p. 181; Kaplan 2022, p. 207), Zingiberaceae Lindl., nom. cons. (Lindley 1835, p. 69), and Typhaceae Juss. (de Jussieu 1789, p. 25; Kubitzki 1998a). Exceptionally, a similar feature ("more or less forming a pseudostem"; Hay and Yuzammi 2000, p. 124) was reported in a representative of Araceae (*Schismatoglottis lingua* A. Hay). Leaf sheaths are a relatively ill-defined character (Bell 2008, p. 72). Several species of the sedge family are rhizomatous (Rodrigues and Maranhão Estelita 2009).

The described fossil plant shows several notable similarities to the Central and South American species *Diplasia karatifolia* Rich. (Cyperaceae, Hypolytreae; Persoon 1805, p. 70). These include: leaves forming pseudostems, leaves in transverse section with very large subrectangular air chambers, very small epidermal cells, and rather thin abaxial and adaxial chlorenchymata. Differences include a subcontinuous layer of sclerenchymatous cells (abaxial hypodermis) in *Diplasia* and relatively thicker septa (Metcalfe 1971, pp. 232–234, fig. 32L–N). The inflorescence of *D. karatifolia* consists of spikelets with spirally arranged glumes (Goetghebeur 1998, p. 161), not unlike the possible spikes found at Rátka.

Another representative of the tribe Hypolytreae, *Mapania bancana* (Miq.) Ridl. [≡ *Thoracostachyum bancanum* (Miq.) Kurz; Miquel 1861, p. 604; Kurz 1869, p. 76; Ridley 1897, p. 258], has also wide leaves with conspicuous air chambers, transversely septate plates of lignified stellate cells. However, the leaves are keeled in *M. bancana*, and large-sized vascular bundles occur throughout the width of lamina (Metcalfe 1971, p. 519, fig. 65H) unlike their location in the abaxial region of the leaves of *R. huberi*.

Several other members of the sedge family have leaves with relatively large air chambers, for example *Carex vulpina* L. (Cariceae; Linnæus 1753, p. 973; Mądalski 1930, pl. 292, fig. 8), *Rhynchospora ciliolata* Boeck. (Schoeneae; Böckeler 1873, p. 563; Martins and Scatena 2011, fig. 1a), *Carpha alpina* R. Br. (Schoeneae; Brown 1810, p. 230; Metcalfe 1971, fig. 16H), *Machaerina angustifolia* (Gaudich.) T. Koyama (Schoeneae; Gaudichaud-Beaupré 1826, p. 417; Koyama 1956, p. 62; Metcalfe 1971, fig. 49E), *Macrochaetium hexandrum* (Nees) H. Pfeiff. (Schoeneae; Nees von Esenbeck 1834, p. 300; Pfeiffer 1931, p. 186; Metcalfe 1971, fig. 51E), and possibly some representatives of *Hypolytrum* Rich. ex Pers. (Hypolytreae; Persoon 1805, p. 70; Baas in Metcalfe 1971, pp. 303, 307). Similar anatomy occurs also in *Typha* L. (Linnæus 1753, p. 971; Mikulska 1977, pl. 594, fig. 12; pl. 595, fig. 11; Müller-Doblies and Müller-Doblies 1977, fig. 159a) and, to a lesser extent, in some Lemnaceae Gray, nom. cons. (Gray 1802, p. 729; Keating 2002, fig. 79B, E). However, all Typhaceae possess a distichous arrangement of the leaves (Kubitzki 1998b) and the Lemnaceae are evidently irrelevant for the Miocene plant due to differences in architecture.

In summary, several features of the studied plant are in agreement with its cyperaceous affinities and none of the features is in contradiction therewith. Even the presumed spikes, although discarded in the previous analysis, would fit into such a reconstruction, being quite similar in general aspect either to the spikelets of *Diplasia karatifolia* or to the spikes of *Eleocharis palustris* (L.) Roem. et Schult. (Roemer and Schultes 1817, p. 151; Jermy *et al.* 2007, p. 123). Several monocotyledonous families (Gramineae, Restionaceae, Zingiberaceae, Typhaceae) can clearly be ruled out, but some groups remain as less likely possibilities. An araceous affinity seems unlikely on account of the general leaf morphology; representatives of the Araceae do usually possess a midrib, although there seem to be exceptions (Keating 2002, p. 30). Other arguments for the systematic placement of *R. huberi* from the Miocene of Rátka are conjectures not based on anatomical evidence, insofar as they heavily rely on elimination of successive taxa, in some cases based on less significant features, whereas the existence of extinct genera exhibiting characters out of the scope of the variation present in modern representatives of a family cannot be excluded.

Finally, the question of the applicability of the results outlined above to other plant fossils described under the genus name *Rhizocaulon* should be discussed. First of all, the type species, as selected here, is based on fossil rhizomes. It remains thus to be seen whether in the topotypic material physical connection with leaves can be found and, if so, whether the leaves are of the same type as those described here. Otherwise the genus should be understood as a fossil-genus for monocotyledonous rhizomes, in which case it would include organs of plants belonging nearly certainly to several families of the natural system, insofar as "the rhizome provides but a few characters of taxonomic interest" (Metcalfe 1971, p. 29). For example, Neogene rhizomes described as species of *Rhizocaulon* were subsequently interpreted as representatives of the Zingiberaceae (Kownas 1959; Worobiec and Lesiak 1998; Fischer *et al.* 2009; Kowalski 2016). Zingiberaceous affinities can be ruled out for *R. huberi* from Rátka on account of the phyllotaxis (in the Zingiberaceae the leaves have a distichous arrangement; Tomlinson 1969, p. 398).

NOMENCLATURE OF THE GENUS *RHIZOCAULON*

The genus *Rhizocaulon* and its authorship

Currently the genus name *Rhizocaulon* is most often used for anatomically preserved (permineralised) rhizomes of monocotyledons (e.g., Worobiec and Lesiak 1998; Kvaček and Wilde 2006; Gregor 2008; Fischer *et al.* 2009; Gregor *et al.* 2010). As briefly signalled by Thomas (2015) and shown in more detail hereafter, there are several problems, both nomenclatural and palaeobotanical, associated with this name. The following discussion is devoted solely to the nomenclatural aspects of the question, insofar as the proposing of any definitive solution would require examination of the material described by Gaston de Saporta which comes from southern France; this is out of the scope of the present study.

The generic name *Rhizocaulon* appeared in print for the first time in several places in Oswald Heer's book on Tertiary flora and climate (Heer 1861; see also Schumann 1893, p. 228). It was mentioned six times in a chapter devoted to the Tertiary floras of Provence (southern France) written by Gaston de Saporta (1861, pp. 135, 136, 160, 163, 165, 166) and once in the text written by Heer (1861, p. 130). Henry Andrews, the author of a widely used catalogue of fossil plant genera, was of the opinion that the genus name was validly introduced in the above-mentioned 1861 book (Andrews 1955, p. 228; 1970, p. 184), in which the following species were named: *Rhizocaulon gracile* Saporta (Heer 1861, p. 130), *R. macrophyllum* Saporta (Saporta 1861, p. 135), *R. polystachium* Saporta (Saporta 1861, p. 136), and *R. recentius* Saporta (Saporta 1861, pp. 160, 166). The first two species were found in the beds with brown coal near Fuveau and Auriol (local stage F *sensu* Heer 1861), the age of which is Late Cretaceous ('Fuvelian', local name for terrestrial Campanian strata). *Rhizocaulon polystachium* was named on the basis of plant fossils from the environs of St. Zacharie (local stages L and M; Eocene?), whereas *R. recentius* from the region of Manosque, is still younger (local stages S and T; Miocene?), as indicated by its name (Latin *recentius*, newer, more recent). Andrews (1955, p. 228) selected *R. macrophyllum* as the type species of the genus, misattributing an Eocene age to this material.

However, the modern rules of nomenclature are stricter than the former usage, and in several cases effective publication is not sufficient to be valid. In particular, valid publication of a taxon requires a meaningful diagnosis (Art. 38.1 of the ICN). Kvaček and Wilde (2006) were of the opinion that this requirement had not been met with by de Saporta (1861) and this genus was validly introduced only in a subsequent publication (de Saporta 1862). This position was followed by Fischer *et al.* (2009, p. 402). Gaston de Saporta's monograph on the Tertiary floras of Provence was published in ten parts between 1861 and 1874 (a detailed list with dates of publication is given by Zeiller 1895, p. 374). In the second part of the monograph (de Saporta 1862) the following taxa are given Latin diagnoses: the tribe Rhizocauleae Saporta (de Saporta 1862, p. 193; « au moins une tribu », "at least a tribe", p. 197) and two species, *Rhizocaulon macrophyllum* (de Saporta 1862, p. 198; pl. 1, fig. 4) and *Rhizocaulon subtilinervium* (de Saporta 1862, p. 199; pl. 1, fig. 5), both from the Campanian of the environs of Aix-en-Provence. *Rhizocaulon brongniartii* (lower Oligocene; Zeiller 1900, p. 289) is described in detail (in French, no diagnosis) and three figures are provided (pl. 1, figs 1–3). However, a diagnosis for the genus was not given, insofar as the tribe Rhizocauleae was intended to be monotypic and so "the characters of the genus need not be defined" [« Ce groupe (…) constitue au moins une tribu bien distincte, qui ne comprend que le seul genre *Rhizocaulon* dont les caractères, par conséquent, n'ont pas besoin d'être définis », p. 197]. From the point of view of the present rules of nomenclature, however, this means that none of these names were validly published in the 1862 paper:

– the genus is not published validly, because a diagnosis is not given;
– species are not published validly, because the genus name is not published validly (*diagnosis generico-specifica* would work only for a monotypic genus; Art. 38.5 of the ICN);
– the tribe name is not published validly, because it is based on an illegitimate genus name.

The nomenclatural aspect of the treatment of the genus *Rhizocaulon* in the famous treatise by Wilhelm Philipp Schimper, entitled *Traité de paléontologie végétale* (Schimper 1870–1872, pp. 418, 420) is quite the same as above. The Rhizocauleae are treated as a family, but for the same reasons as in de Saporta (1862), neither the family, nor the genus or any of its species are validly published.

Another palaeobotanical treatise, called *Paläophytologie*, belonging to the series *Handbuch der Paläontologie* edited by the palaeozoologist Karl A. Zittel, was published in nine fascicles between 1879 and 1890 (Stafleu and Cowan 1985, p. 138). Here a description referring precisely to the genus *Rhizocaulon* (with credit to de Saporta) is given on pp. 390–391 and in the opinion of the present authors this constitutes the first valid publication of the genus name. The discussed treatise, according to the title page was 'begun' by W.P. Schimper and 'continued' by A. Schenk. It has not been possible to establish the authorship of this part of the text, so it is referred as Schmiper and Schenk (1879–1890), following the model of citation in Kvaček *et al.* (2021, p. 131); the corresponding fascicle (Lief. 4, pp. 333–396) was published in 1885 (Stafleu and Cowan 1985). The conclusion of this part of the somewhat fastidious investigation is that the authorship of the discussed genus is as follows: *Rhizocaulon* Saporta ex Schimp. et Schenk, Handb. Palaeont., Palaeophyt., p. 390 [Lief. 4, 1885]. The three following names are illegitimate: *Rhizocaulon* Saporta in Heer, Rech. climat vég. tert., p. 135 [1861], nom. illeg.; *Rhizocaulon* Saporta, Ann. Sci. nat., 4^{e}, 17, p. 197 [1862], nom. illeg.; and *Rhizocaulon* Saporta ex Schimp., Traité paléont. vég., p. 418 [1870], nom. illeg. A few other papers dealing with *Rhizocaulon* may be briefly overviewed from the point of view of nomenclature. There exists a French translation of the treatise on palaeophytology (Schimper and Schenk 1891). The corresponding part (pp. 379–380) does not differ in any significant aspect from the earlier German edition.

Schumann (1893) considered that *R. brongniartii* is a typical representative of the genus, but he did not present a diagnosis or formally select a type species. A description of the genus is given in Zeiller (1900, p.

289) and two species are named (*R. brongniartii* and *R. polystachyum*).

The type species of *Rhizocaulon*

In the protologue of the genus (Schimper and Schenk 1879–1890) three species are mentioned: *R. brongniartii* (rhizome), *R. polystachyum* (stem), and *R. gypsorum* (leaf). None of them is described by any term suggesting that it should be preferred for selecting the type. In order to preserve the current understanding of the genus (see above), *Rhizocaulon brongniartii*, based on a rhizome, is selected herein as the type of the genus. Re-investigation of the types of this species, coming from the Oligocene of Southern France, is out of the scope of the present paper. The genus is either a fossil-genus for fossil rhizomes, if connection with other structures (leaves) cannot be proven (a 'form genus'), or a more restricted genus for monocotyledon plants, if otherwise; this question may be resolved only after a lectotype has been selected for the type species, a problem out of the scope of the present paper.

The typification by Andrews (1955) who selected *R. macrophyllum* as the type species of the genus is null, insofar as it refers to an invalidly published species. Gregor *et al.* (2010, p. 5) listed the genus "*Rhizocaulon* Saporta 1862" with a "generotypus (?): *Rhizocaulon gypsorum* Saporta, Ann. Sci. Nat. Bot., Ser. 4, 17: 222–223, Taf. 4 Fig. 1, 1862". This sentence with a quotation mark indicating doubt is not taken as a valid designation of a type species. In any case, it would refer to an illegitimate name, so it would be null as well.

The question of the affinities of the studied plants (i.e., *R. huberi*) is treated above; this should, however, be distinguished from the question of the affinities of the fossil-genus *Rhizocaulon* which may be heterogeneous in terms of a natural system. This is why in the systematic part the genus is classified as *incerti ordinis* and *incertae familiae*. As explained above, this question is out of the scope of the present investigation, depending upon restudy of the type species, including the selection of a lectotype.

CONCLUSIONS

Rhizocaulon huberi H.-J. Gregor is re-investigated on the basis of the Miocene material coming from the type locality at Rátka, Hungary, including rhizomes, roots, and leaves. Microscopic preparations were made for the first time. The plant is reconstructed as consisting of a rhizome with roots arising from all sides and containing tristichously arranged leaves forming a pseudostem. In the roots, the primary cortex has radial strands of tissue separated by lacunae of schizogenic origin or resulting from tangential lysigeny. The leaves are dorsiventral; their interior consists mostly of an aerenchyma; vascular bundles possess an abaxial phloem.

The new whole plant reconstruction presented here is significantly different from that published in the protologue (Gregor 2008). In particular, specimens showing presumed lateral ramifications of the rhizome, partitioned by transverse septa and with whorled roots (Gregor 2008, fig. 1E; pl. 4, fig. 4; pl. 6, fig. 4), have never been found in organic connection with the rest of this material, and are interpreted here as belonging to a different plant species.

The tristichous phyllotaxis of leaves in specimens of *Rhizocaulon huberi* (physical connection observed) is a valuable systematic character, allowing us to exclude the affinities of the studied plants with either the Gramineae (proposed as one of the possibilities in the protologue) or the Restionaceae. The Juncaceae are ruled out on account of the pseudostem. The studied plant is likely to belong to the Cyperaceae (especial similarities are noted with *Diplasia* Rich.), but this cannot be proven conclusively.

The analysis of the oldest published works in which the genus name *Rhizocaulon* is used leads to the conclusion that both the genus name *Rhizocaulon* and all its species used by de Saporta (1861, 1862) are invalidly published (diagnosis lacking; ICN, Art. 38.1).

The genus *Rhizocaulon* was first validly published by Schimper and Schenk (1879–1890), so the correct authorship is *Rhizocaulon* Saporta ex Schimp. et Schenk, Handb. Palaeontol., Palaeophyt., p. 390 [Lief. 4, 1885].

Rhizocaulon brongniartii Saporta ex Schimp. and Schenk, a Cainozoic permineralised rhizome from Southern France, is selected as the type species of the genus *Rhizocaulon*. The typification made by Andrews (1955) refers to a species that was not validly published, so is null and void.

The interpretation of the systematic affinities of the Rátka plant should not be uncritically extended to other representatives of the genus *Rhizocaulon*. This question should be solved after re-study of the type material of the genus.

Acknowledgments

Krzysztof Dembicz (Warszawa) is acknowledged for his help during fieldwork. JK thanks the technical service of the

Institute of Paleobiology of the Polish Academy of Sciences for help during the preparation of polished sections and microscopic preparations. ATH warmly thanks Alexander Sennikov (University of Helsinki) and Julia Gravendyck (University of Bonn) for providing detailed comments on nomenclatural matters, as well as Michael Rummel (Naturmuseum Augsburg) for arranging the restudy of the types and Dario De Franceschi (Muséum national d'Histoire naturelle, Paris) for information on de Saporta's material. The reconstruction was skilfully drawn by Bogusław Waksmundzki (Faculty of Geology, University of Warsaw). Reviews by Shirley Martins (Universidade Estadual do Oeste do Paraná) and Ruth Stockey (Oregon State University) are gratefully acknowledged.

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Manuscript submitted: 25th July 2025
Revised version accepted: 15th November 2025

PLATES 1–17

PLATE 1

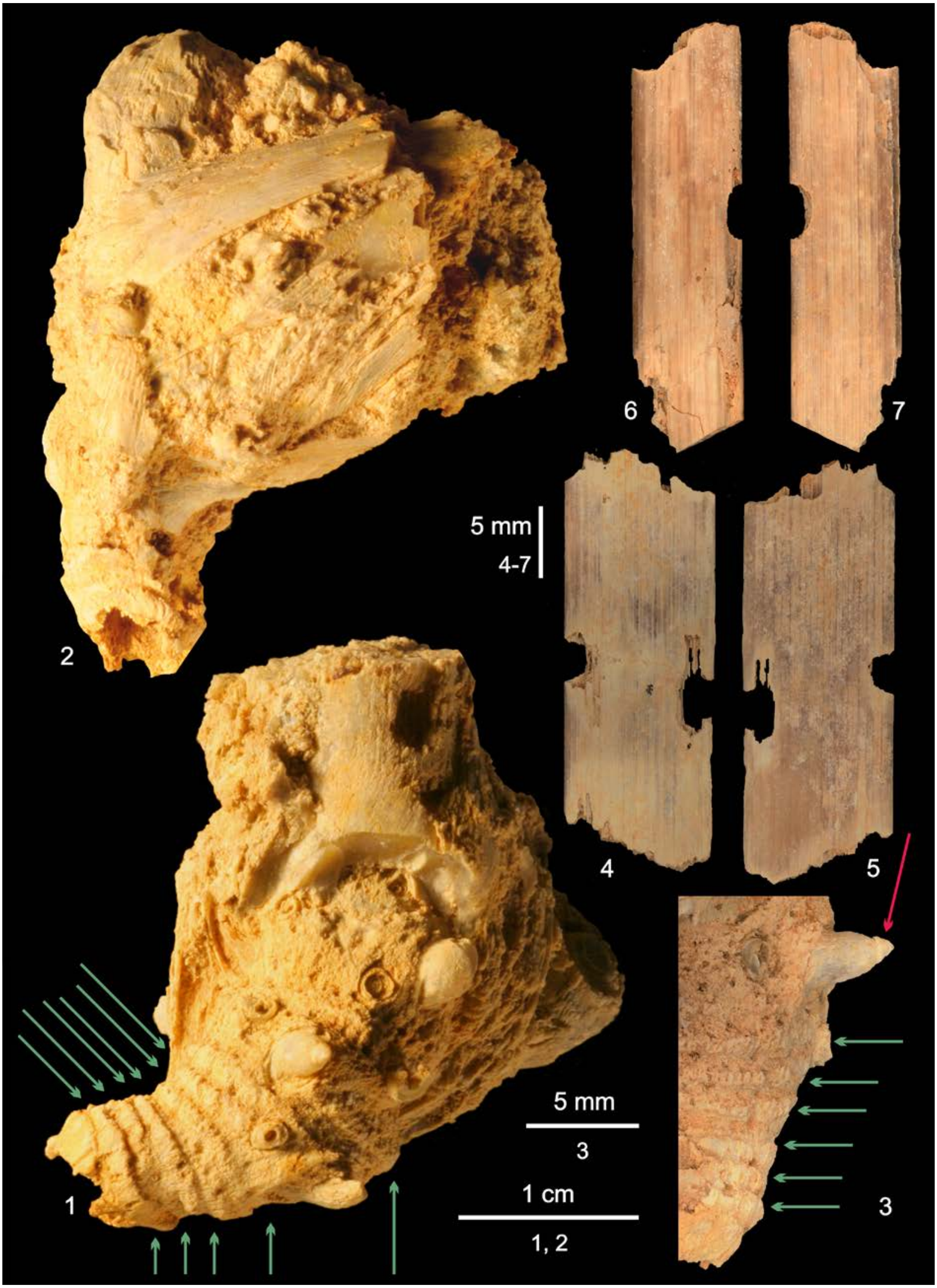
General views of *Rhizocaulon huberi* H.-J. Gregor

1–**3** – rhizome MWGUW ZI/119/1. 1, 2 – general views from two sides; 3 – enlargement of fragment showing root with root cap. Green arrows show cataphylls on nodes of rhizome; red arrow shows the root cap.

4, **5** – leaf fragment MGWUW ZI/119/18. 4 – adaxial view; 5 – abaxial view.

6, **7** – leaf fragment MGWUW ZI/119/21, views of leaf folded in half, both sides representing abaxial (convex) surface.

All specimens are from the Miocene of Rátka, Hungary.


6
7
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1 cm
1, 2
3

PLATE 2

Rhizomes of *Rhizocaulon huberi* H.-J. Gregor

Polished transverse sections of permineralised rhizomes observed in reflected light. 1 – MWGUW ZI/119/5; 2 – MWGUW ZI/119/3 (see Plate 3 for enlargement); 3 – MWGUW ZI/119/4; 4 – MWGUW ZI/119/2 (see Plate 4 for enlargements).

All specimens are from the Miocene of Rátka, Hungary.

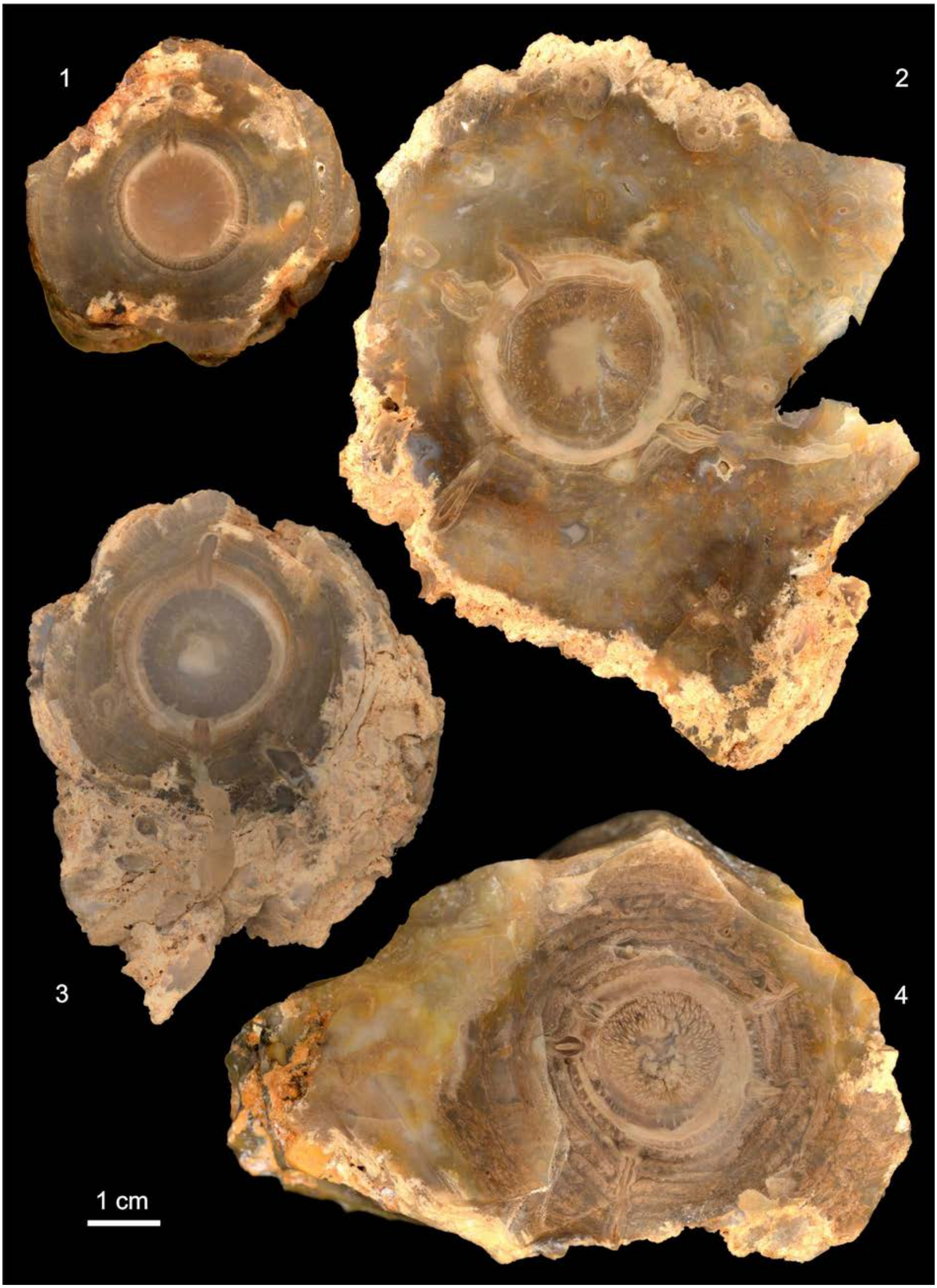

1
2
3
4
1 cm

PLATE 3

Rhizomes of *Rhizocaulon huberi* H.-J. Gregor

Polished transverse section of permineralised rhizome, MWGUW ZI/119/3, surrounded by leaves (cataphylls); enlargement of rhizome with emerging roots (compare Pl. 2, Fig. 2).

Legend: ct – cataphyll (successive cataphylls numbered and thickness shown).

Specimen is from the Miocene of Rátka, Hungary.

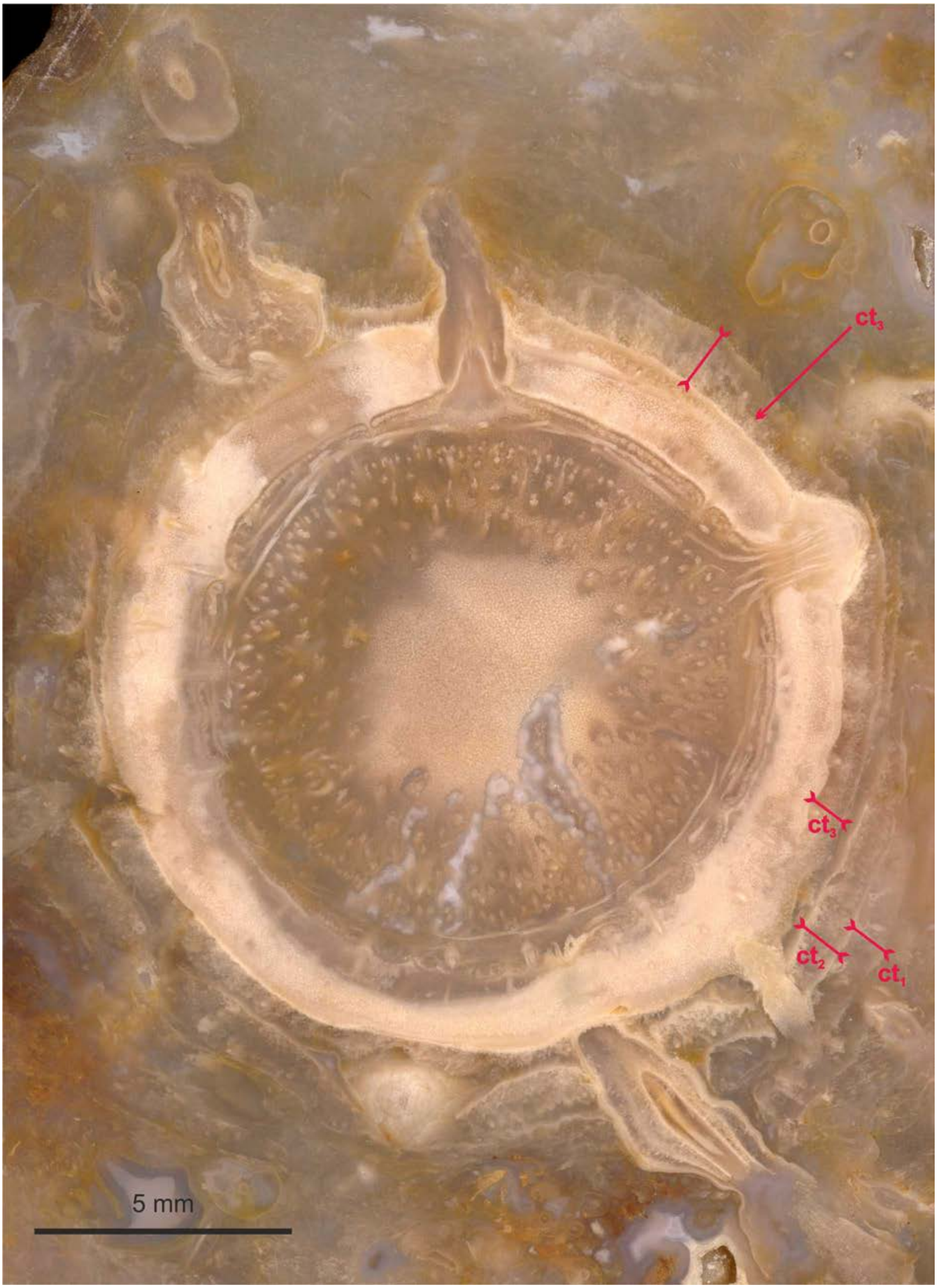

ct$_3$
ct$_3$
ct$_2$
ct$_1$
5 mm

PLATE 4

Rhizomes of *Rhizocaulon huberi* H.-J. Gregor

Polished transverse section of permineralised rhizome, MWGUW ZI/119/2 (compare Pl. 2, Fig. 4). 1 – enlargement of rhizome with emerging roots; 2 – enlargement of emerging roots.

Specimen is from the Miocene of Rátka, Hungary.


2
5 mm


1
5 mm

PLATE 5

Rhizomes of *Rhizocaulon huberi* H.-J. Gregor

Polished longitudinal section of permineralised rhizome, MWGUW ZI/119/6.

Specimen is from the Miocene of Rátka, Hungary.


1 cm

PLATE 6

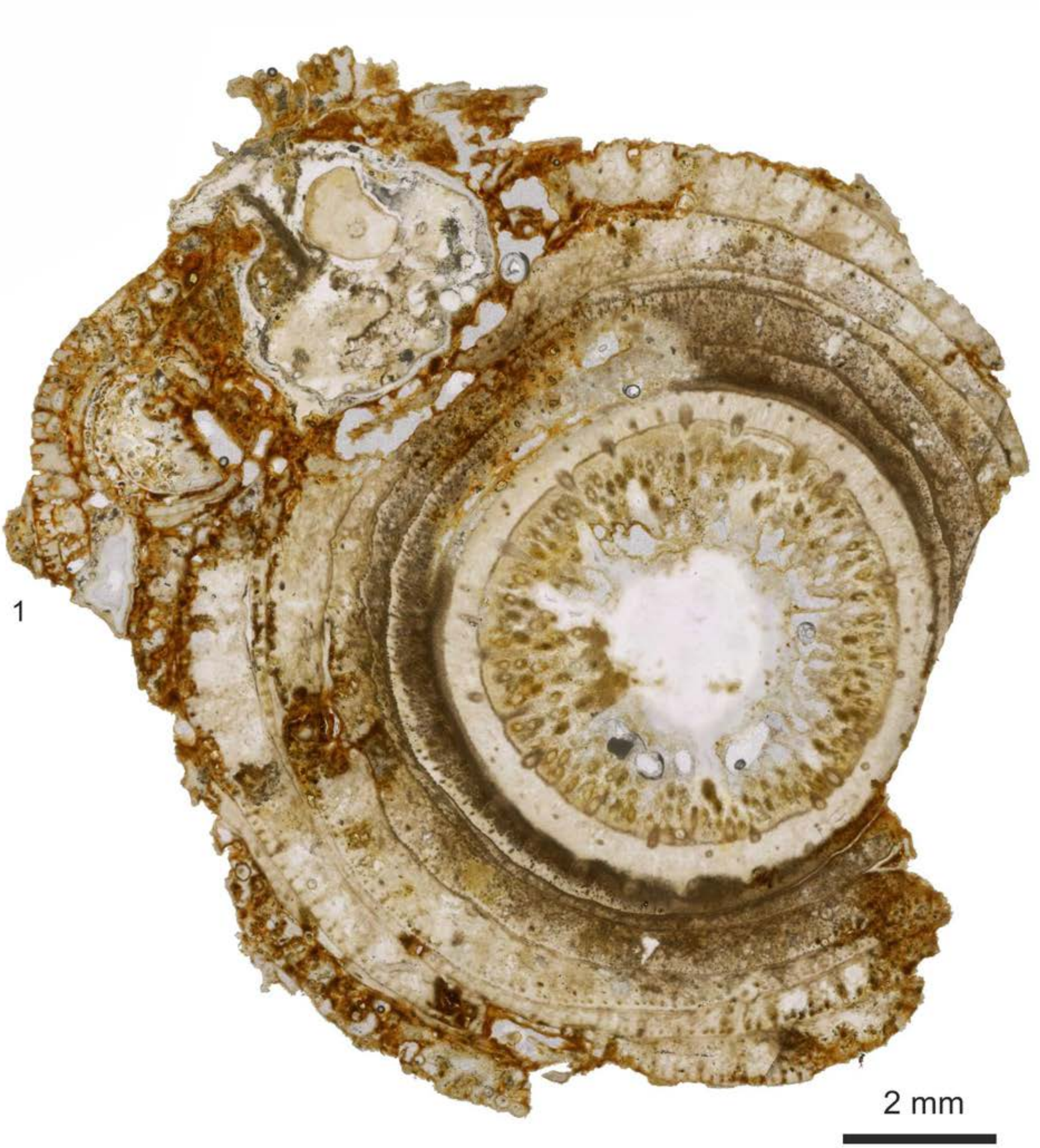
Rhizomes of *Rhizocaulon huberi* H.-J. Gregor

Microscopic preparation of permineralised rhizome, MWGUW ZI/119/7C, observed in transmitted light (compare Pl. 7). 1 – general view; 2 – enlargement of fragment with explanatory symbols.

Legend: d – rhizodermis and hypodermis; e – endodermis; f_1, f_2, f_3, f_4 – leaves surrounding the rhizome; ic – internal cortex; m – central zone of amorphous silica, possibly corresponding to area in which medullary parenchyma was not preserved; mc – median cortex; vb – vascular bundles.

Specimen is from the Miocene of Rátka, Hungary.

1



2

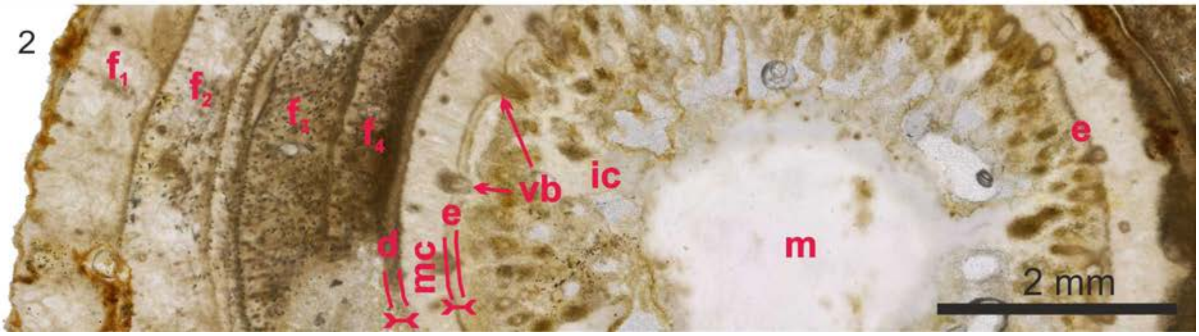


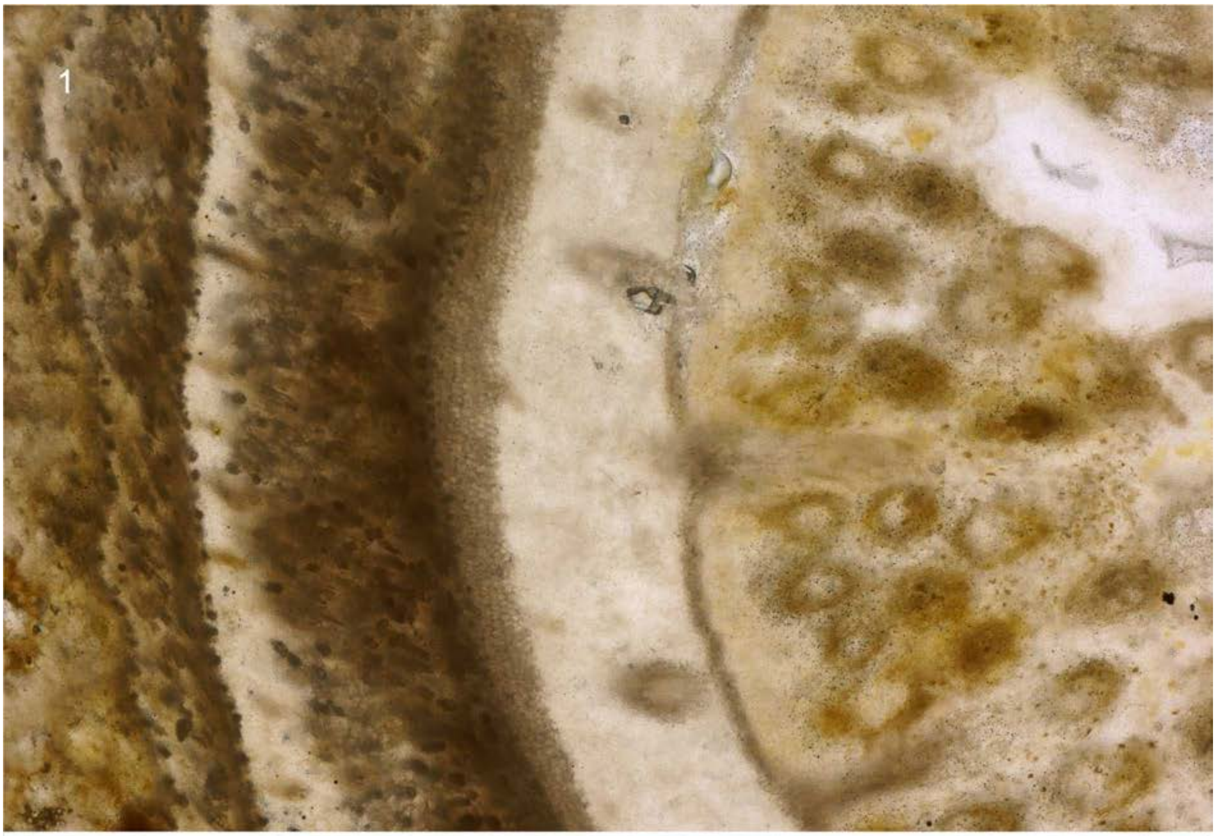
PLATE 7

Rhizomes of *Rhizocaulon huberi* H.-J. Gregor

Microscopic preparation of permineralised rhizome, MWGUW ZI/119/7C, nlargements of fragments observed in transmitted light; compare Pl. 6 for general view.

Legend: e – endodermis; f_1, f_2, f_3, f_4 – leaves surrounding the rhizome; h – hypodermis; ic – internal cortex; m – central zone of amorphous silica, probably corresponding to area in which medullary parenchyma was not preserved; mc – median cortex; r – rhizodermis; vb – vascular bundles.

Specimen is from the Miocene of Rátka, Hungary.


1

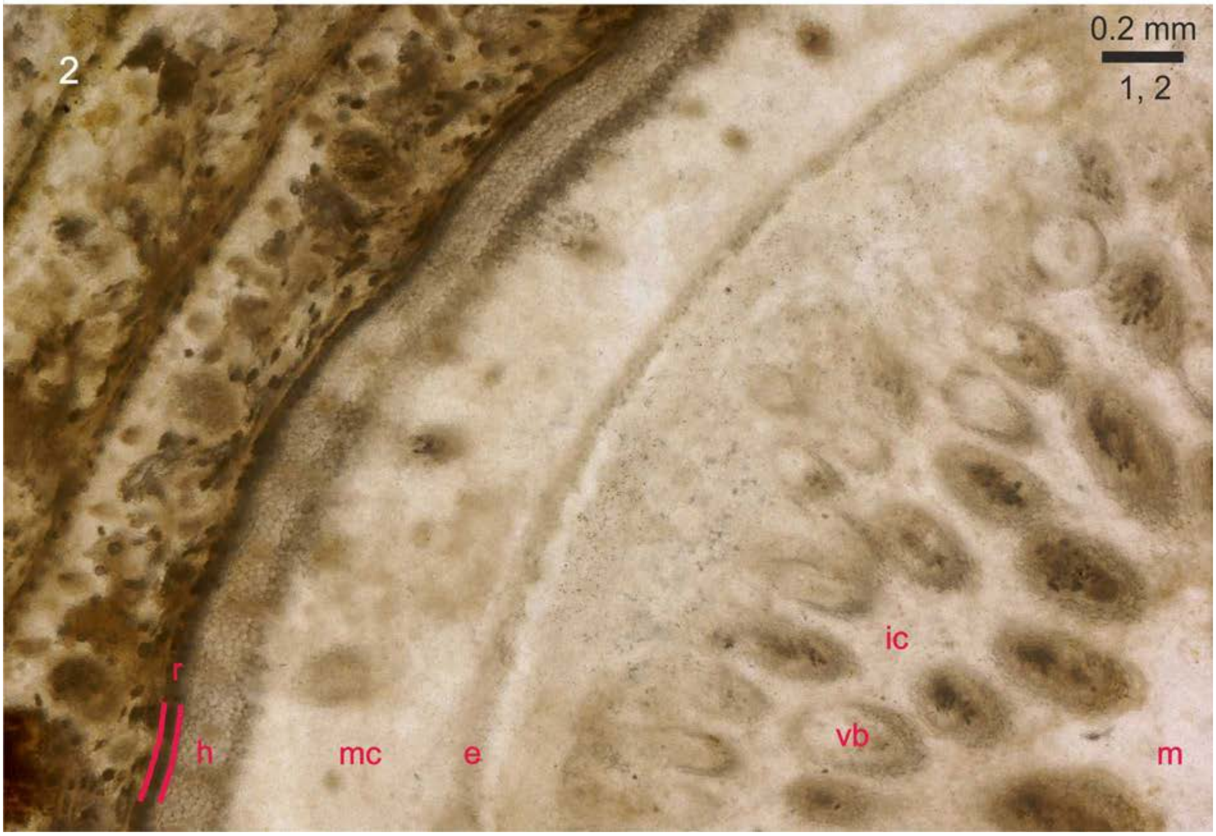

2
0.2 mm
1, 2
ic
r
vb
h
mc
e
m

PLATE 8

Roots of *Rhizocaulon huberi* H.-J. Gregor

Microscopic preparation of permineralised rhizome, MWGUW ZI/119/8, observed in transmitted light. 1 – general view; 2, 3 – enlargements of roots. See Pl. 9 for further enlargements.

Specimen is from the Miocene of Rátka, Hungary.

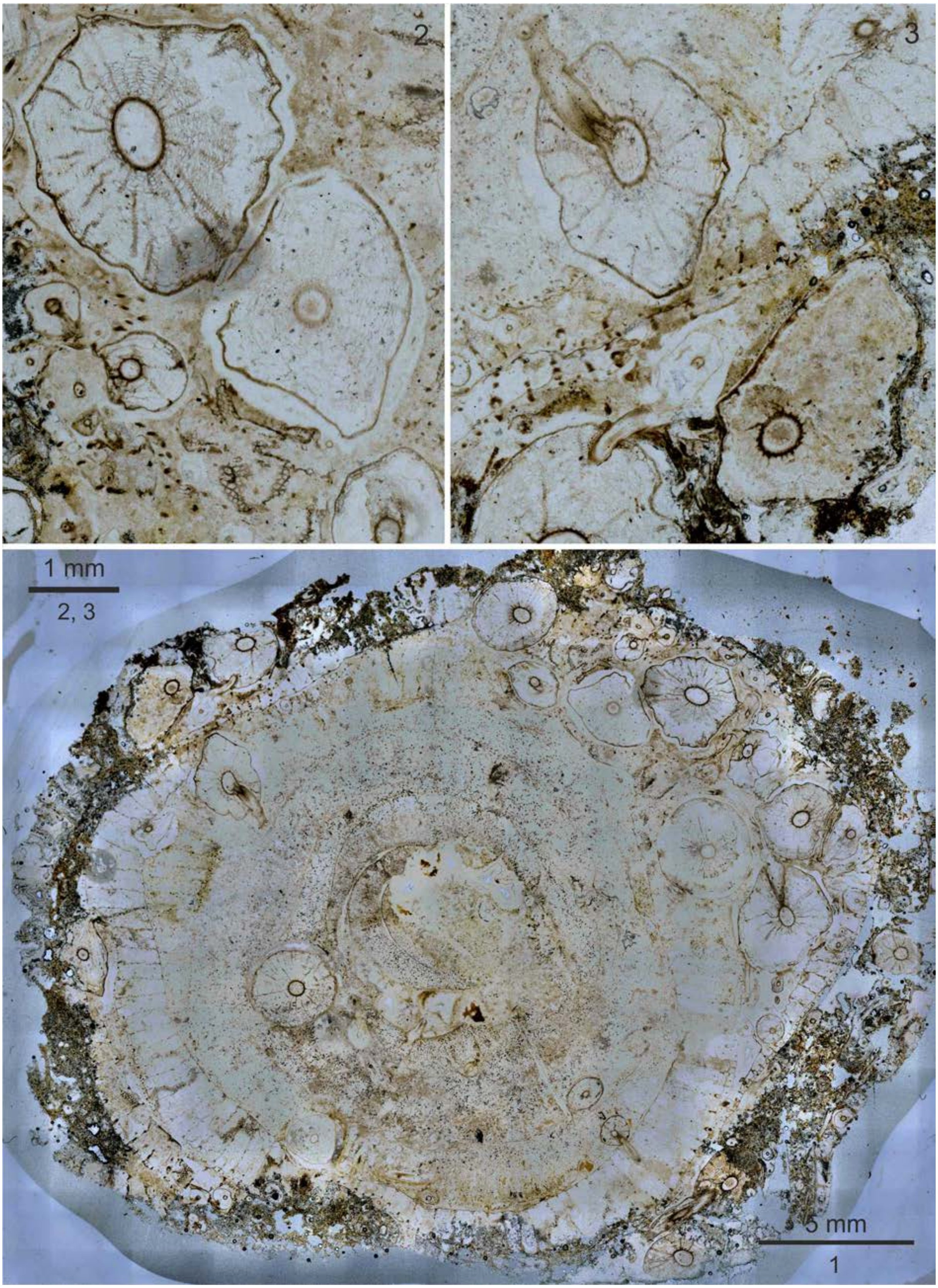

2
3
1 mm
2, 3
5 mm
1

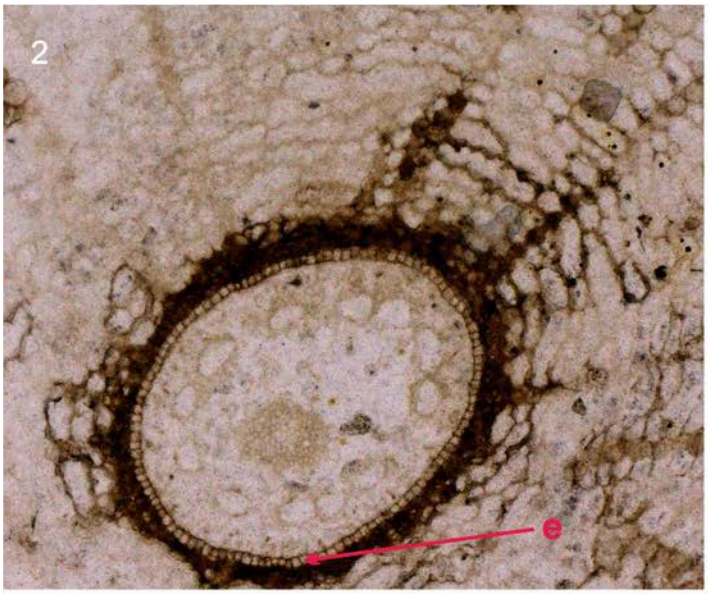
PLATE 9

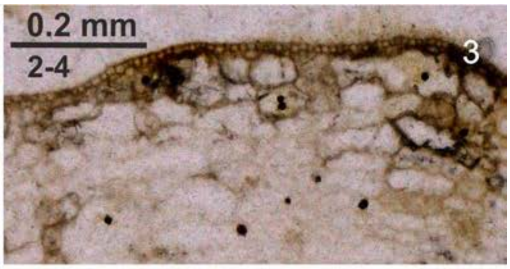
Roots of *Rhizocaulon huberi* H.-J. Gregor

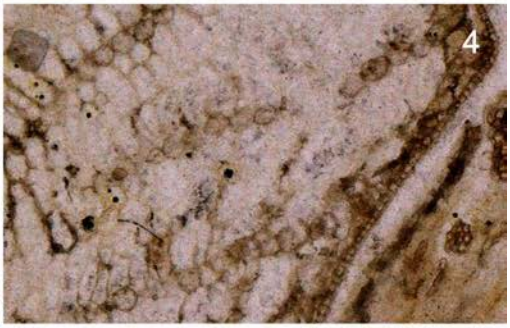
Microscopic preparation of permineralised rhizome, MWGUW ZI/119/8, observed in transmitted light (see Pl. 8 for general view). 1 – general view; 2 – enlargement of stele; 3 – enlargement of external part with epidermis; 4 – enlargement of parenchyma showing effects of lysigeny.

Legend: e – endodermis.

Specimen is from the Miocene of Rátka, Hungary.


2
e


0.2 mm
2-4
3


4


1
0.2 mm

PLATE 10

Roots of *Rhizocaulon huberi* H.-J. Gregor

Polished transverse section of rhizome, MWGUW ZI/119/9, with enlargement of root with root cap. 1 – general view of rhizome; 2 – enlargement of emerging root with root cap.

Specimen is from the Miocene of Rátka, Hungary.


1
2 mm


2
2 mm

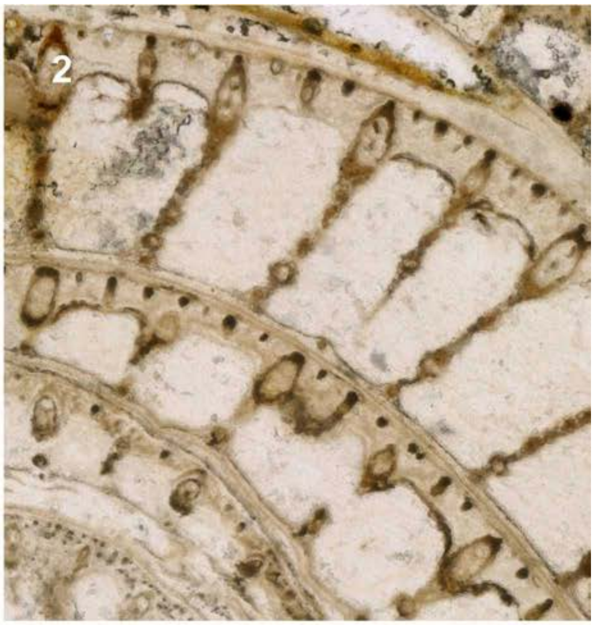
PLATE 11

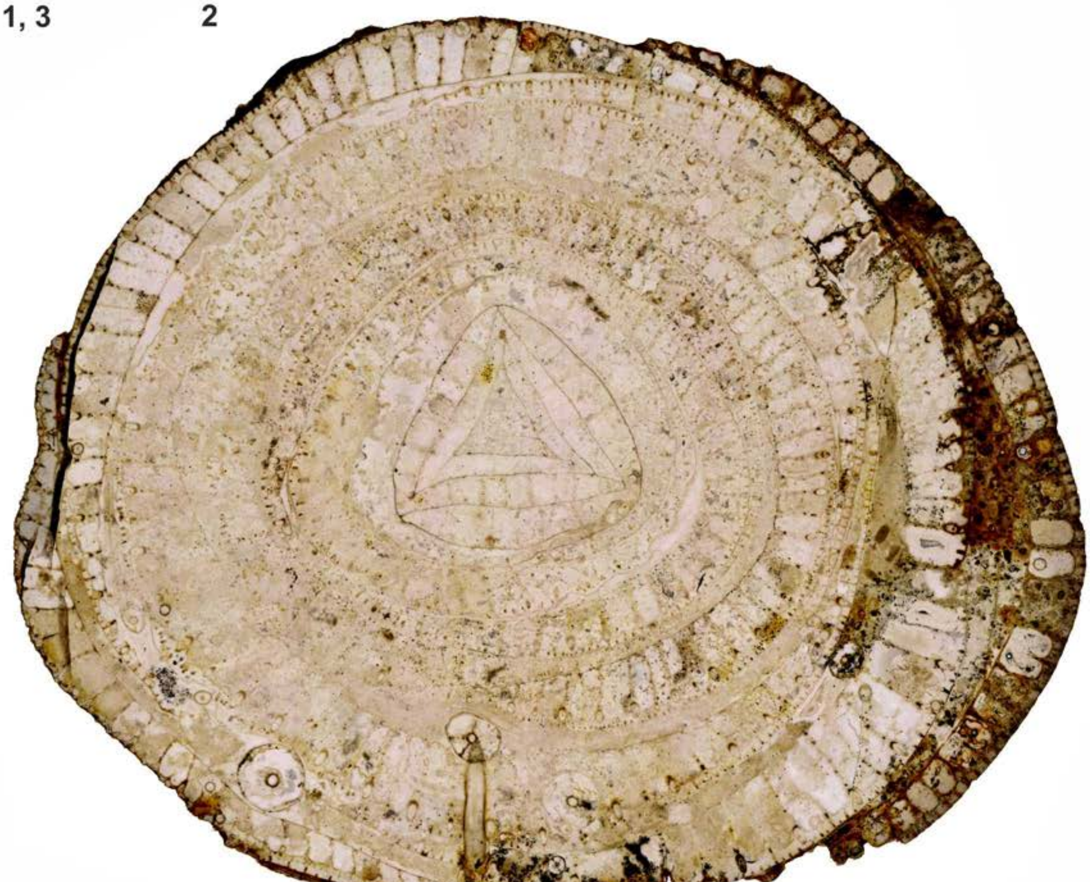
Leaves of *Rhizocaulon huberi* H.-J. Gregor

Microscopic preparations of pseudostems formed by leaves (euphylls) in tristichous disposition. 1, 2 – MWGUW ZI/119/7A, general view and partial enlargement showing three leaves stacked on one another; 3 – MWGUW ZI/119/12B, general view.

All specimens are from the Miocene of Rátka, Hungary.

1





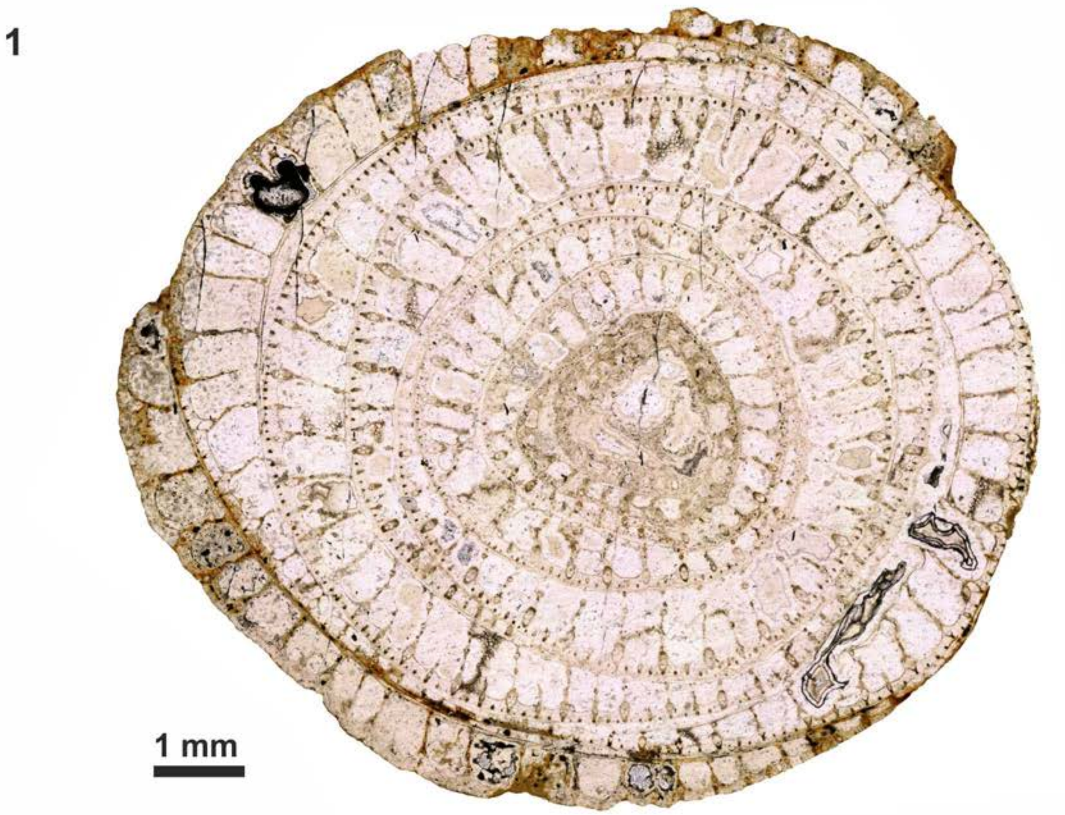
3

PLATE 12

Leaves of *Rhizocaulon huberi* H.-J. Gregor

Microscopic preparation of pseudostem formed by leaves in tristichous disposition, MWGUW ZI/119/10. 1 – general view; 2 – partial enlargement showing leaves tightly stacked on one another.

Specimen is from the Miocene of Rátka, Hungary.


1
1 mm

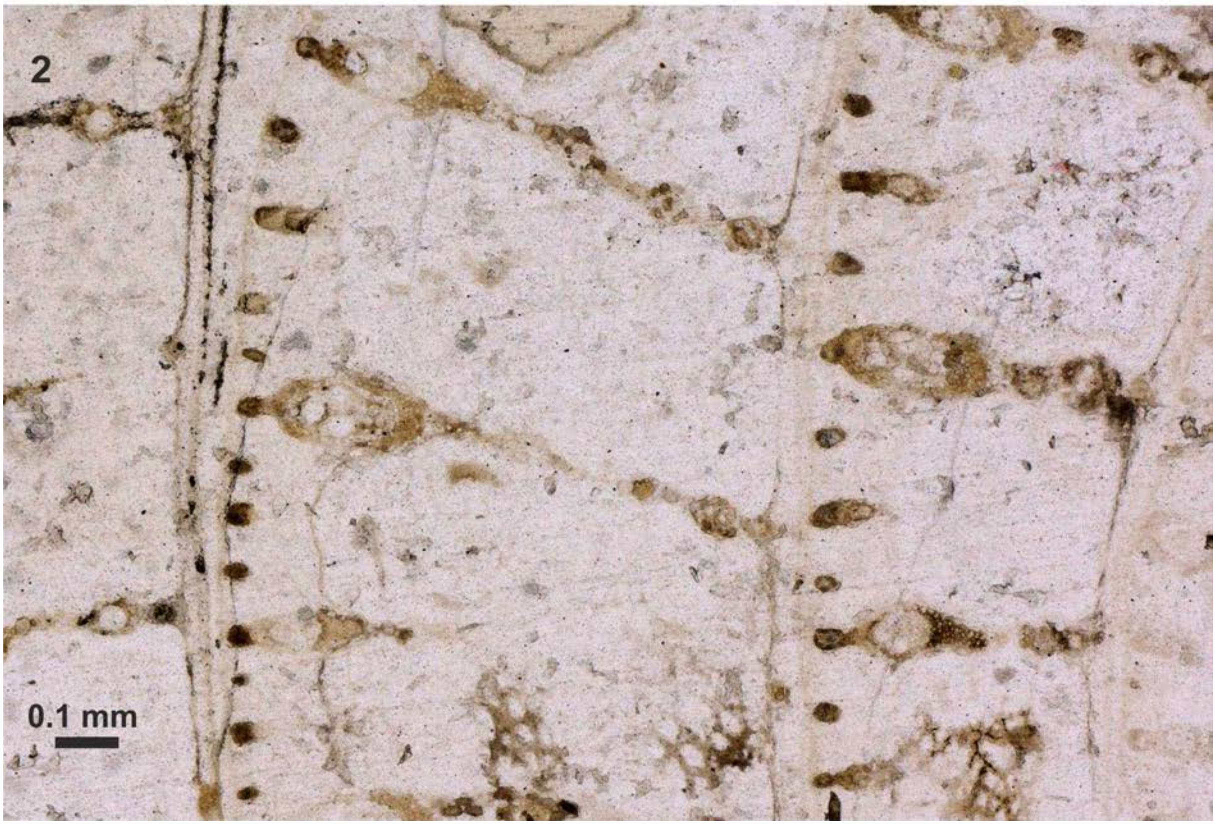

2
0.1 mm

PLATE 13

Leaves of *Rhizocaulon huberi* H.-J. Gregor

Transverse section of leaves forming pseudostem; microscopic preparation, MWGUW ZI/119/11, observed in transmitted light (see Pls 14, 15 for enlargements).

Specimen is from the Miocene of Rátka, Hungary.

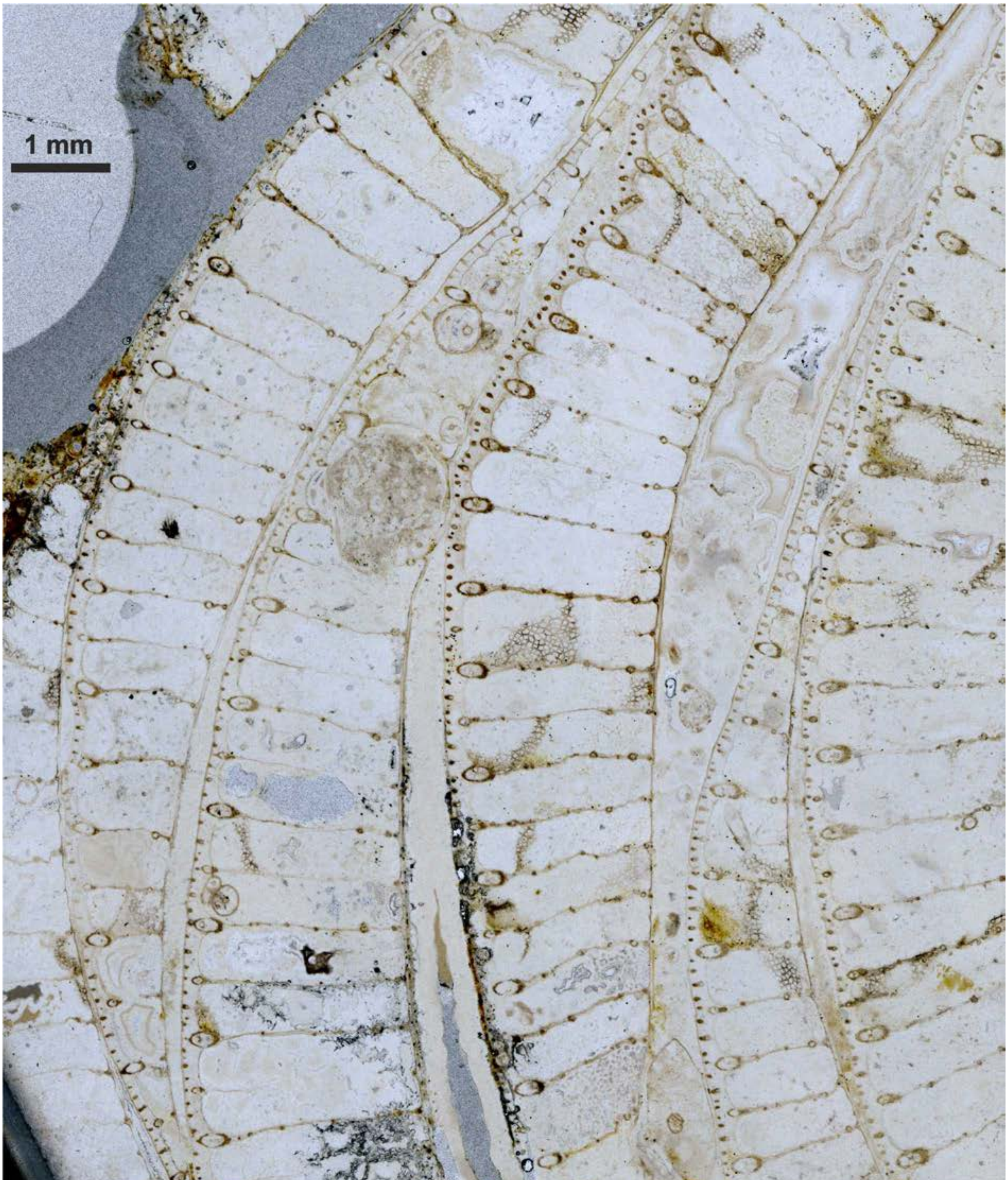

1 mm

PLATE 14

Leaves of *Rhizocaulon huberi* H.-J. Gregor

Transverse section of leaves forming pseudostem; microscopic preparation, MWGUW ZI/119/11, observed in transmitted light (see Pl. 13 for broader view and Pl. 15 for further enlargement). Blue and orange arrows show that main and small vascular bundles regularly alternate in abaxial chlorenchyma. Violet arrow indicates total thickness of leaf; most of it is taken by air chambers.

Legend: ae – air chambers; di – diaphragm with stellate cells; eb – abaxial epidermis; ed – adaxial epidermis; p – parenchyma (chlorenchyma); rt – root; sp – transverse septum between air chambers; vbm – main vascular bundle; vbn – minor vascular bundle; vbs – small vascular bundles in abaxial chlorenchyma; vbt – small vascular bundles in septa between air chambers.

Specimen is from the Miocene of Rátka, Hungary.

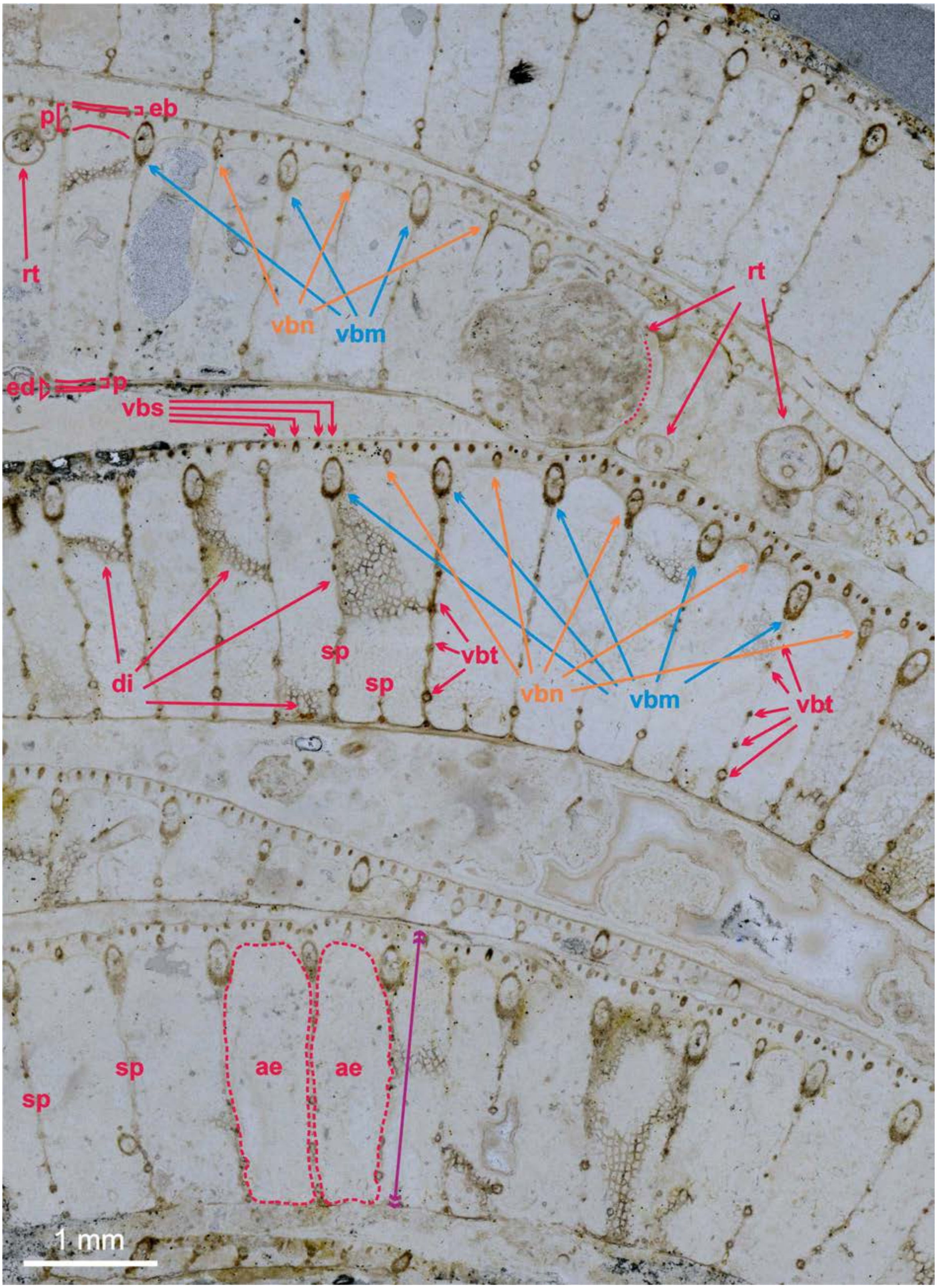

p
eb
rt
vbn
vbm
ed
p
vbs
rt
di
sp
sp
vbt
vbn
vbm
vbt
sp
sp
ae
ae
1 mm

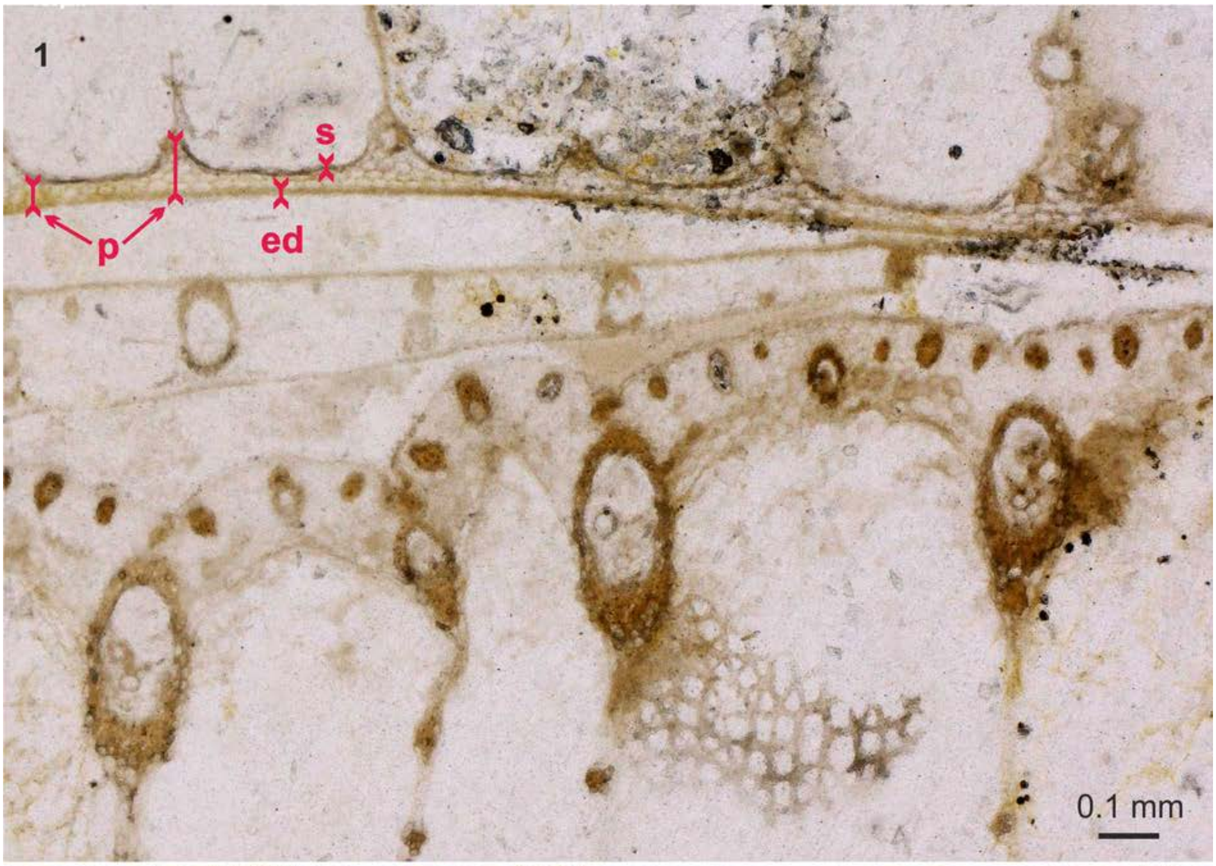
PLATE 15

Leaves of *Rhizocaulon huberi* H.-J. Gregor

Microscopic preparation, MWGUW ZI/119/11 (see Pls 13, 14 for broader views), enlargements of transverse sections.

Legend: ed – adaxial epidermis; p – parenchyma (here: adaxial chlorenchyma; cellular details visible only in single leaf); s – possible sclerenchyma fibres. Note numerous diaphragms in air chambers.

Specimen is from the Miocene of Rátka, Hungary.


1
s
p
ed
0.1 mm

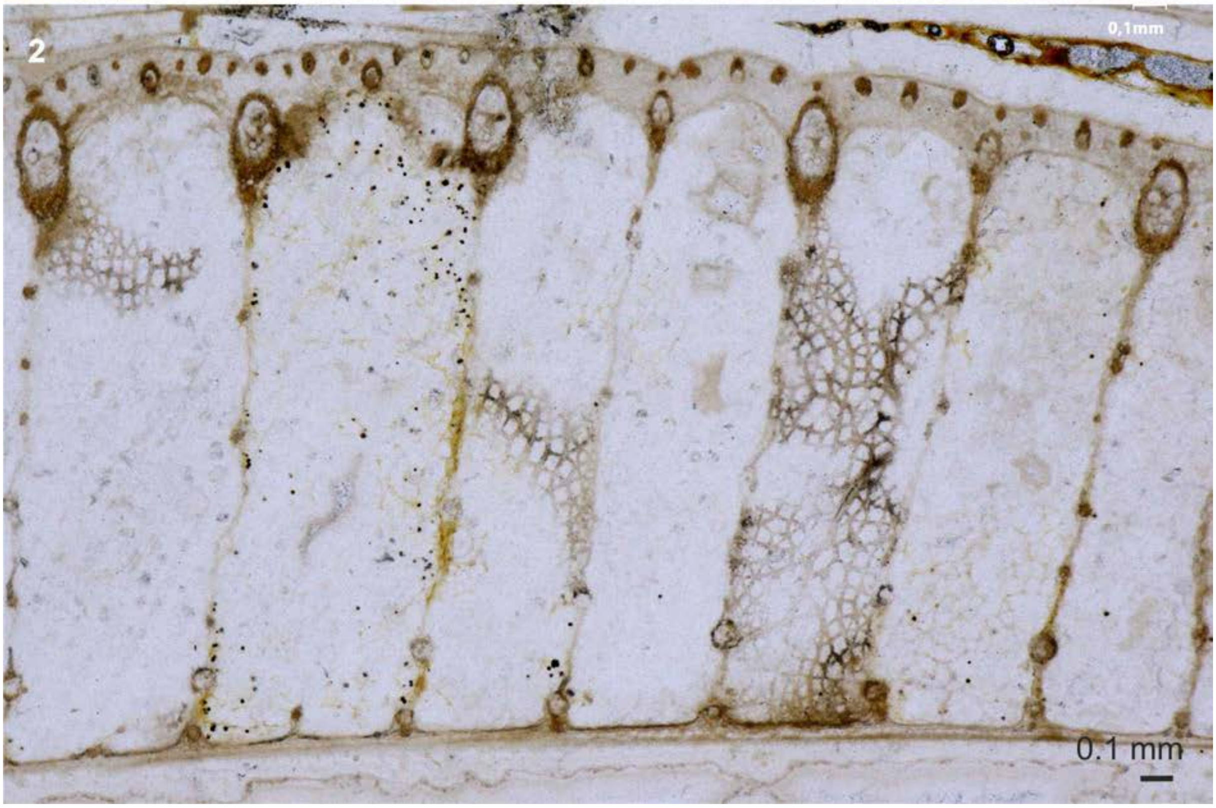

2
0,1mm
0.1 mm

PLATE 16

Leaves of *Rhizocaulon huberi* H.-J. Gregor

Microscopic preparation, MWGUW ZI/119/20, enlargements of transverse sections.

Legend: di – diaphragm with stellate cells; eb – abaxial epidermis; ms – mestome sheet; mx – metaxylem; p – parenchyma (here: abaxial chlorenchyma); ph – phloem; ps – parenchyma sheet; px – protoxylem; sg – sclerenchyma girder; sp – transverse septum between air chambers; vbm – main vascular bundle; vbn – minor vascular bundle; vbs – small vascular bundle; vbt – smaller vascular bundle in septa between air chambers.

Specimen is from the Miocene of Rátka, Hungary.

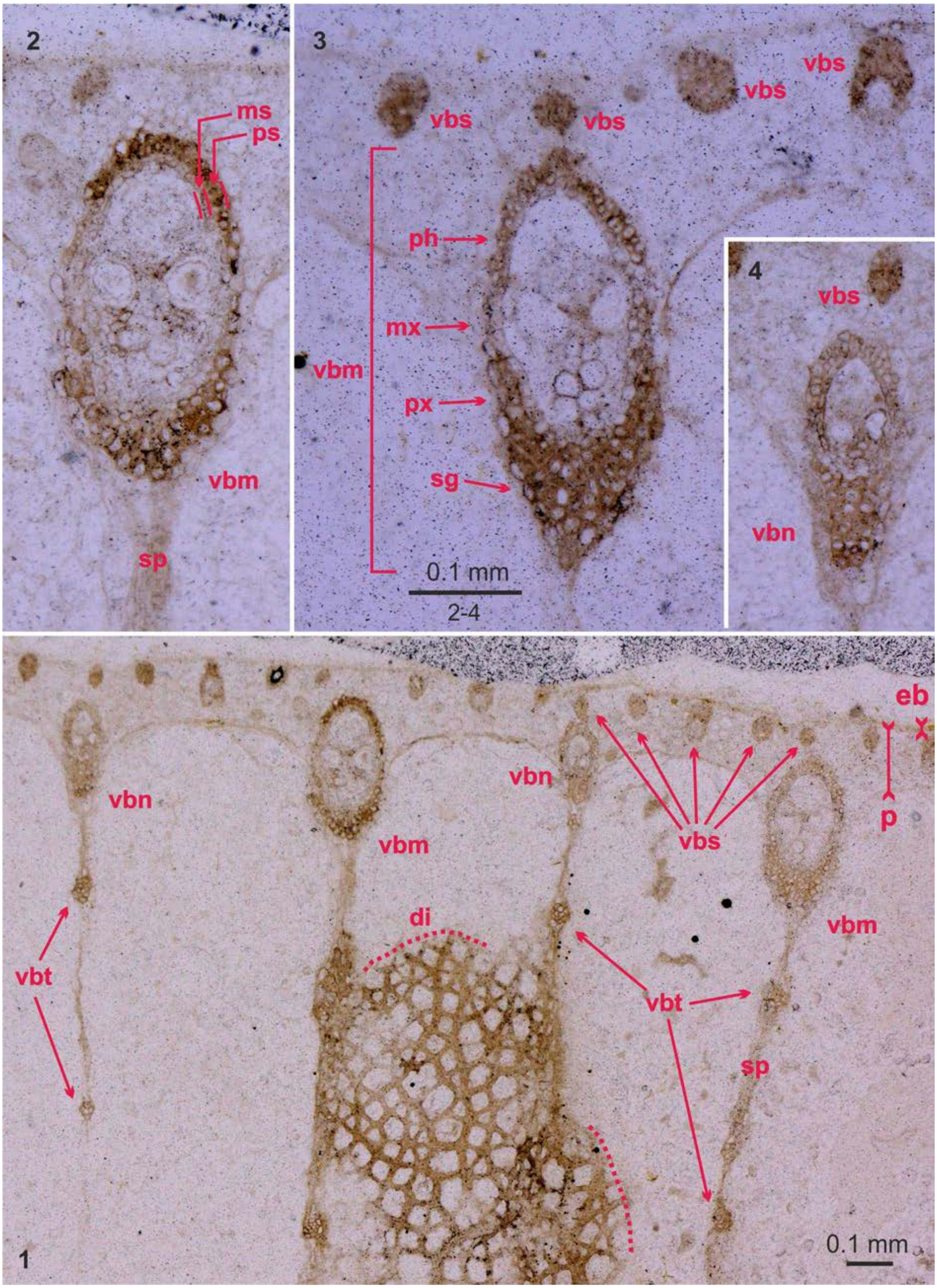

2
ms
ps
vbm
sp
3
vbs
vbs
vbs
vbs
ph
mx
vbm
px
sg
0.1 mm
2-4
4
vbs
vbn
vbn
vbm
vbn
vbs
eb
p
vbm
di
vbt
vbt
sp
0.1 mm
1

PLATE 17

Spike associated with *Rhizocaulon huberi* H.-J. Gregor

Specimen MWGUW ZI/119/19, three spikes or spikelets trapped between halves of leaf folded in half, not in organic connection with any other part of the described material. 1 – general view of specimen; 2 – enlargement of spikes.

Specimen is from the Miocene of Rátka, Hungary.


1
5 mm


2 mm
2