


Mosses from Rovno amber (Ukraine), 6. New genus of the family Pylaisiadelphaceae


MICHAEL S. IGNATOV^{1,2*}, DMITRY V. VASILENKO^{3,4}, ANDREI A. LEGALOV^{5,6}
& EVGENY E. PERKOVSKY⁷

¹Lomonosov Moscow State University, Faculty of Biology, Plant Ecology and Geography Dept., Leninskie Gory Str. 1–12, Moscow 119234 Russia.  <https://orcid.org/0000-0001-6096-6315>


²Tsitsin Main Botanical Garden, Russian Academy of Sciences, Botanicheskaya Str., 4, Moscow 127276 Russia.

³Borissiak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya 123, Moscow 117997, Russia;
 <https://orcid.org/0000-0002-4827-7290>

⁴Cherepovets State University, Lunacharsky Prospect 5, Cherepovets 162600, Russia.

⁵Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences, 630091 Novosibirsk, Russia;  <https://orcid.org/0000-0001-7347-8169>

⁶Department of Forestry and Landscape Construction, Tomsk State University, 634050 Tomsk, Russia.

⁷Natural History Museum of Denmark, Universitetsparken 15, Copenhagen 2100, Denmark;
 <https://orcid.org/0000-0002-7959-4379>

*Corresponding author. E-mail: misha_ignatov@list.ru

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Abstract

Rovno and Baltic amber inclusions are known as a rich source of late Eocene mosses. Most of them are either referred to extant genera or placed in form-genera with names meaning similarity to an extant taxon. The present moss from Rovno amber is rather exceptional, having combination of features different from any extant mosses known for us. Therefore it is described as *Rovnohypnum* gen. nov., characterized by medium-sized plants, non-branched shoots that are attenuate to their tips, moderately loosely foliate, leaves spreading, ovate, acuminate, cordate at base, costa double, cells elongate, with one to three prominent papillae on dorsal surface, smooth or much weaker papillose on ventral side, proximal branch leaves subdivided into subfilamentose lobes. Putative brood filaments are noticed in many leaf axils. We compare this moss with the Pylaisiadelphaceae, where the brood filaments, pluripapillose cells, and filamentose or subfilamentose structures surround the branch primordia. However, these traits are characteristic for different genera of the family, thus we refer it in a new genus within the Pylaisiadelphaceae.

Key words Fossil mosses, taxonomy, Europe, Eocene, *Rovnohypnum*.

Introduction

Rovno amber is synchronous with the Baltic amber (Perkovsky *et al.* 2007), and its localities are situated less than a thousand kilometers to the south (Chemyreva *et al.* 2024). Despite of the general similarity in flora and fauna (Perkovsky *et al.* 2024), there are a number of differences (Perkovsky 2018),

especially on the species level, e. g. in well-studied trichopteran fauna only 24% of species are common with Baltic amber (Melnitsky *et al.* 2025), and in less studied beetle fauna even only 15% (Telnov & Perkovsky 2025). Among bryophyte syninclusions, the hepatics are especially diverse, with many species and some genera unknown from the Baltic amber (Konstantinova *et al.* 2012; Mamontov *et al.* 2013, 2015a,b,c, 2017, 2018, 2019, 2020, 2024a,b,c,d, 2025).

Mosses were first found in Rovno amber by Ignatov & Perkovsky (2011). That collection and also some subsequent studies (Ignatov and Perkovsky, 2013; Ignatov *et al.*, 2016, 2019a,b) revealed a principal similarity between the moss flora from the Rovno amber forest and the Baltic one, as summarized by Ignatov *et al.* (2019b). Most mosses from the European Eocene amber were either referred to extant moss genera or placed in form-genera with names meaning similarity to one or several extant moss genera. Only one moss, *Pottiodicranum* (Ignatov *et al.* 2016) represents the case where it was difficult to place a moss in a family, as some its features contradicted Pottiaceae, while others contradicted Dicranaceae s.l. In previously undescribed collection from Rovno amber we found another example of a moss having combination of traits quite different from any extant mosses known for us. Therefore it appears to be of exceptional interest, and it is described and discussed in the present paper.

Materials and methods

The studied amber specimen is a part of the Rovno amber collection of the Schmalhausen Institute of Zoology in Kiev (SIZK-L-659). The age of Rovno amber is late Eocene, about 35–37 Ma (see discussion in Mitov *et al.* 2021; Perkovsky *et al.* 2007, 2010; Radchenko *et al.* 2021; Chemyreva *et al.* 2024). The specimen was collected in former Vladimirets District between Voronki village and sea Luko. Vladimirets District and other mining areas that now belong to Varash District were the sources of the most interesting Rovno amber inclusions in the last ten years (e. g., Perkovsky & Olmi 2018; Perkovsky & Makarkin 2019; Lyubarsky & Perkovsky 2020; Perkovsky *et al.* 2020; Gilka *et al.* 2021; Golub *et al.* 2021; Jałoszyński & Perkovsky 2021; Matalin *et al.* 2021; Perkovsky & Nel 2021; Olmi *et al.* 2022; Yamamoto *et al.* 2022; Belokobylskij *et al.* 2023; Kirichenko-Babko & Perkovsky 2023; Fedotova *et al.* 2024; Kirichenko-Babko *et al.* 2024; Melnitsky *et al.* 2024).

After primary preparation, weight of the amber piece was 2.5 gram; it had polyedric shape of 3.0 x 1.5 x 1.0 cm. The specimen lacks any insect syninclusions and other bryophytes, but one stellate trichome and one putative young fungus or slime mould on moss leaf were recorded.

The moss inclusions in the specimen SIZK-L-659 were studied and photographed using stereomicroscopes: a Nikon SMZ25 equipped with a digital camera, a Nikon DS-Fi3 (Figs. 1, 3A–J), and a compound microscope Olympus BX-63P equipped with a digital camera DP74 (Figs. 2, 3K). To optimize visualization of the three-dimensional inclusions, photomicrographs were combined from several optical sections using the focus stacking software Helicon Focus 8 (Kozub *et al.* 2008) or the focus stacking package EDF built into the NIS-Elements imaging software that controls the Nikon SMZ25.

Systematic paleobotany

Order Hypnales

Family Pylaisiadelphaceae

Genus *Rovnohypnum* Ignatov, gen. nov.

Diagnosis: Plants medium-sized, in loose tufts. Shoots distally non-branched, attenuate, moderately loosely foliate. Leaves spreading, broadly ovate to ovate-lanceolate, acuminate, cordate at base; costa double; cells elongate, distinctly papillose on dorsal side, smooth or much weaker papillose on ventral side. Proximal branch leaves subdivided into subfilamentose lobes.

Type species: *Rovnohypnum papillosum* Ignatov sp. nov.

Etymology: Rovno is city in Ukraine, the place that gave the name to a famous amber source, known as Rovno amber. *Hypnum* is a small genus of mosses now, but in 19th and 20th centuries it was understood sensu lato, including many hundreds of pleurocarpous mosses. Many groups of the former *Hypnum* are classified now in genera which names are formed with '-*Hypnum*' as a second part of the genus name.

The genus includes only one species.

Rovnohypnum papillosum Ignatov, sp. nov.
(Figs. 1–3, 4A–G)

Type: Holotype. L-659 (shoot marked 'H !' in Fig. 1A, also shown in Fig. 4A–G); Rovno amber, late Eocene. Syninclusions: one stellate trichome and only one putative fungus or slime mould in Fig. 2A and its inset (Schmalhausen Institute of Zoology in Kiev).

Etymology: The species name refers to leaf laminal cells that are prominently papillose dorsally.

Diagnosis: Pleurocarpous moss with spreading stem leaves, narrow lanceolate or filiform lobes of proximal branch leaves around branch primordia, papillose laminal cells, and putative brood filaments in leaf axils.

Description: Stems to 9 mm long, 60–120 µm wide, with leaves up to ca. 1 mm wide. Developed branches unknown. Branch primordia 80–140 µm across, outermost foliose structures (hereafter lobes of compound proximal branch leaves) 2–3, connected by a low 'basal membrane', they are 70–200 µm long, at base 40–50 µm wide, distally uniseriate, filiform, cells in distal part ca. 40 x 10 µm. Paraphyllia absent. Foliage terete, multiseriate, distance between leaves along one orthostich ca. 200 µm, so there are ca. 12 leaves per 1 mm; shoots are attenuate distally. Leaves near shoot tips small, 0.3–0.4 x 0.1–0.15 mm, erect to erect-spreading at ca. 20–30° with the stem and overlaying the leaf above, further downwards leaves are larger, 0.6–0.7(–1.1) x 0.3–0.4 mm, spreading and forming an angle with the stem of 45–90°, almost never overlaying the leaf above; ovate-lanceolate or ovate-triangular, gradually of moderately abruptly acuminate, acumina constituting 0.4–0.6 the leaf length; rather abruptly narrowed to the insertion, somewhat cordate at base, shortly decurrent, concave, so smaller leaves are concave-channeled, while larger leaves are irregularly plicate; margins serrate up to base, usually with the distance between teeth 15 µm. Costa double, reaching to about half leaf. Laminal cells 30–45(–60) µm long, 6–13 µm wide, 8–9 µm thick, thick-walled, on dorsal surface papillose, papillae 1 to 3 per cell, large; on ventral surface cell smooth or with small papillae in subapical and submarginal parts of leaves. Putative brood filaments 2–7 in leaf axils, 100–210 x 10 µm, cylindrical, cellular structure hardly discernible.

Material description: The moss shoots are embedded in an amber piece allowing observation and photography from three sides, but one of them is less convenient for photography, so most photos are taken from face shown in Fig. 1A and only two photographs here are from another face (Fig. 1B, C), situated at ca. 90° to the former. One specimen from third face is not shown here, at poorer preserved and having no differences from better seen shoot of other faces.

The amber piece includes ca. 12 moss shoots. Larger shoots are all arranged in one direction, lacking developed branches, but with branch initials in leaf axils. Shoots are quite evenly foliate along their main parts, the leaves are subequal in size and spreading at the broad or almost right angle; however, upwards the leaves are smaller, deviating from stem at acute angle, and in the apical part erect. Two small shoots, with leaves similar to those near tips of larger shoots, are laying separately (Fig. 1A, E, F). Their papillosity patterns are similar to those in leaves from larger shoots, therefore we consider them to be conspecific. Some shoots with larger leaves (Fig. 1B, right and 2A) look slightly different, as the bigger leaves are less spreading, but details of their surface and their leaves in the thinner parts of the stem with more loose foliage indicate the taxonomic identity of all shoots within this amber piece. Variation of leaves from broadly ovate to ovate-lanceolate is a common case in extant mosses, therefore such variation needs no special discussion.

The surface views are to a large extent hampered by the layer of finely granulose cover that is likely a thin layer of air and maybe also some other mineral substances. The moss surfaces are looking minutely papillose in combination with large papillae, which are interpreted as the moss papillae covered with the air layer. The cell outlines are seen only in few places (Figs. 2A, C, 3E, F, M), making possible to measure median laminal cells as 30–45(–60) x 6–13 µm. Marginal cells are somewhat shorter, as

marginal teeth in both large and small leaves (Fig. 3) are at ca. 15 μm one from another. Treansverse lead section in Fig. 4G shows also the cell thickness, of 8–9 μm .

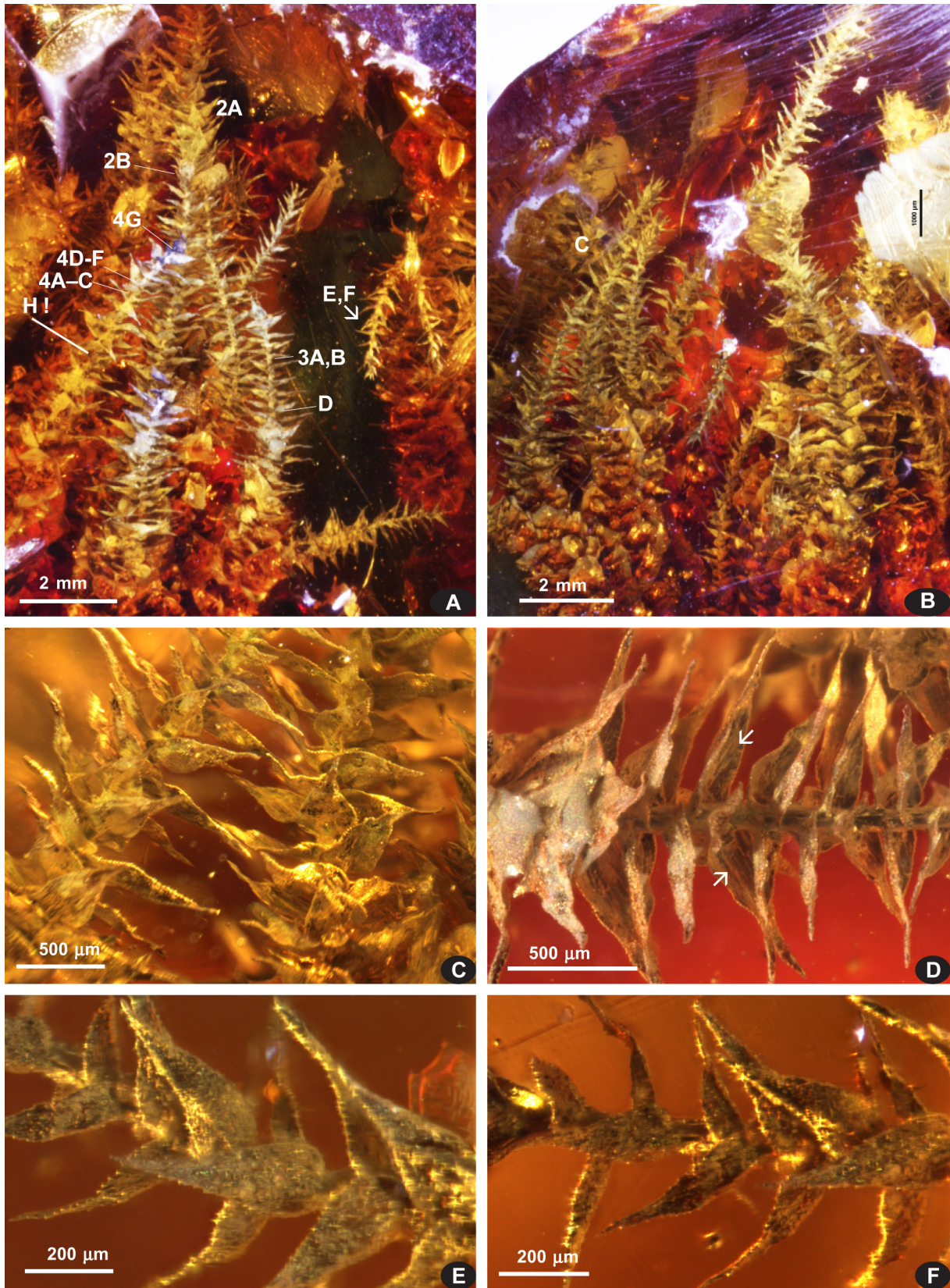


Figure 1. *Rovnohypnum papillosum* gen. et sp. nov. (reflected light): A, B: habit from two faces, at ca. 90° one from another; positions of some further images are marked in A and B; C–F: shoots, showing foliage variation; a putative brood filaments are arrowed in D. The shoot on the right marked as H ! is selected as the holotype (it is shown its details in Fig. 4A–G).

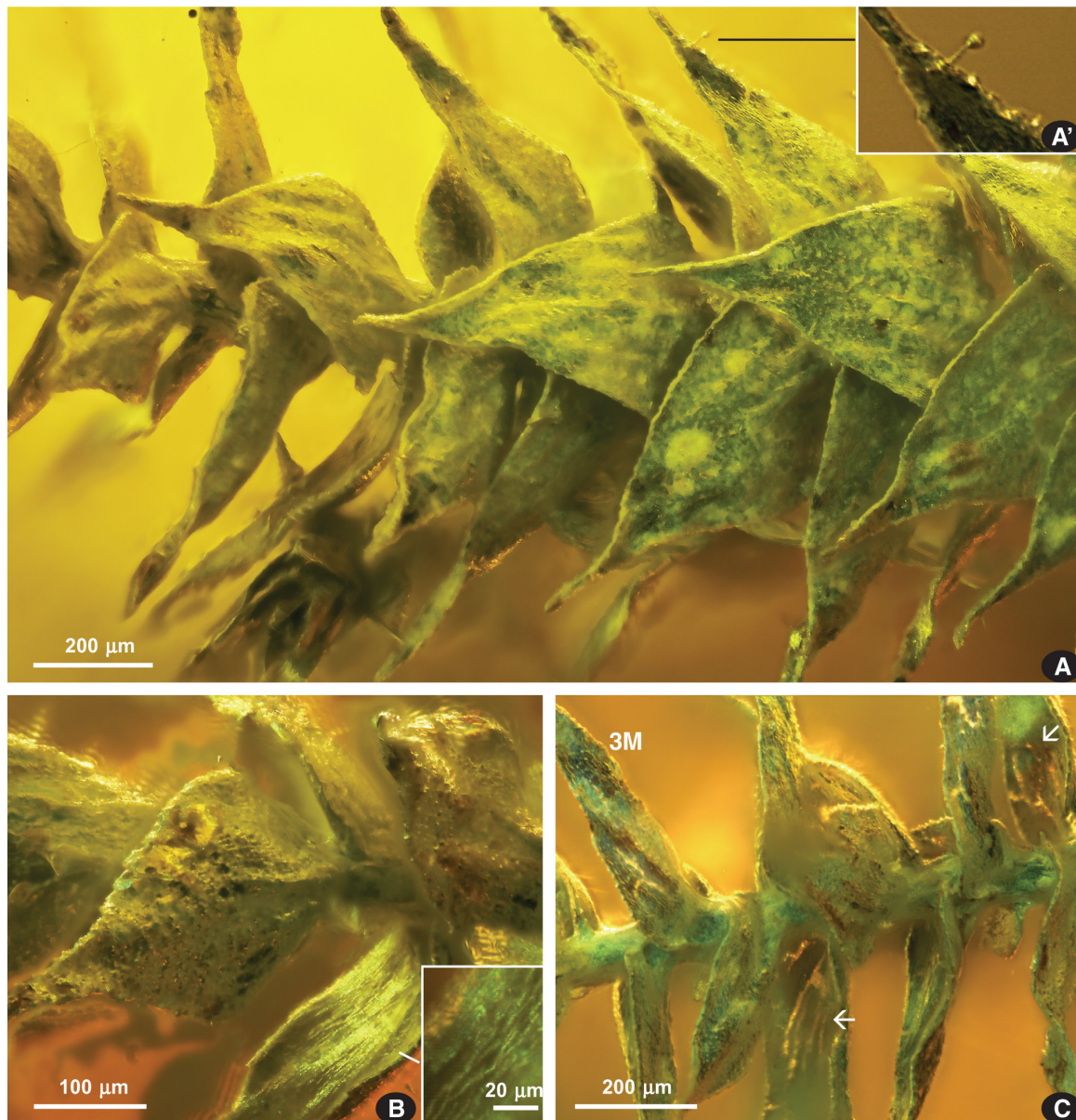


Figure 2. *Rovnohypnum papillosum* gen. et sp. nov. (in transmitted light, showing less conspicuous papillosity at front views). A: median part of long shoot (cf. Fig 1A), showing extensive coverings of silt and similar substances at time of fossilization; a putative fungus or slim mould on the leaf margin is shown in inset; B: leaves near shoot apex (cf. Fig 1A), showing dorsal leaf surface with large papillae and ventral leaf surface with smooth cells in the central part of leaf and smaller papillae in the submarginal part; inset is a close up of the part of ventral surface; C: a subapical part of shoot, with leaves widely spreading, facing putative brood filaments in leaf axils (arrowed); the place magnified in Fig. 3M is marked.

In distal part of leaves some papillae look being single per cells, while in other cells 2–3. These patterns are moderately clearly seen only in few places now very clearly seen (Fig. 3M, arrowed), but in other places they are dense and arranged in a rows at the distance ca. 10–14 µm, which means that papillae are several per cell, as the laminal cell wherever seen are elongate, (25–)30–50(–60) µm long (Fig. 3G, I, L).

Brood filaments remain so far only putative. They are covered by granulose layer (seemingly air), making impossible to discern short cells which apparently form them, if our interpretation of them is correct. The possibility that they are axillary hairs is the least probable, as axillary hairs are too delicate for such preservation ub axils of many leaves. Alternatively, some kind of folds near the costa might look similarly, but their rather regular occurrence in many leaf axils makes this interpretation less probable that the brood filament hypothesis.

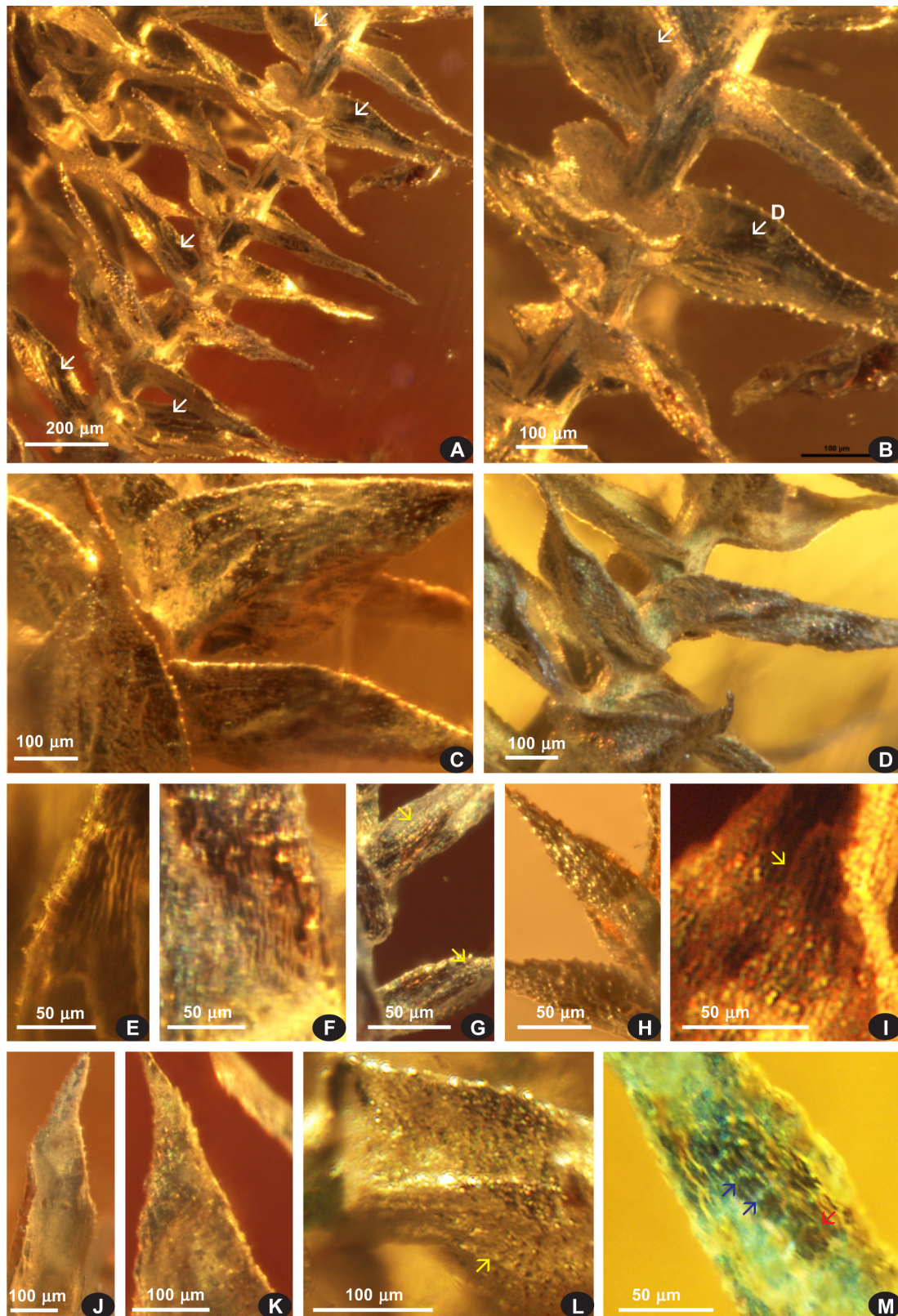


Figure 3. *Rovnohypnum papillosum* gen. et sp. nov. (A–L in reflected light; M in transmitted light). Leaf shape variation, papillosoity patterns and putative brood filaments in leaf axils (arrows). Dorsal view in C shows double costa (and some plicae nearby), E, J, K: ventral side of leaf, other images are from dorsal side. E, F, M: rare cases of partial fell off cover of air layer, disclosing leaf surface and showing elongate cell outlines from ventral (E) and dorsal sides (F, M), the latter are with distinct papillae; G, I, L show areas with seriate papillae, yellow arrow; J: ventral view, not showing surface structures being hidden by air, as in many leaves in other images of this moss; K: ventral view, showing few papillae closer to leaf apex; M: cells with unipapillose (red arrow) and multipapillose cell with 2(?) papillae (blue arrows).

Branch primordia pattern is a trait which may have a crucial importance for the ordinal placement of fossil mosses, as for example in case of the genus *Tricosta* (Shelton *et al.*, 2015). Leaf-like structures, however, are exceedingly difficult to study in fossils, since they are mostly covered by leaves. Loose foliage of *Rovnohypnum* luckily gave the chance to see their details clearly in as much as three leaf axils of the holotype shoot (Fig. 4A–G). The fourth (cf. Fig. 1A, 4A) is not very well seen for its details and therefore not shown in a close up. One primordium in Fig. 4B, is especially well-developed, showing narrow-lanceolate and subfilamentose lobes which comprise proximal branch leaves divided up to the base and therefore treated here as compound branch leaves (often called pseudoparaphyllia, but usage of this term has been challenged as too indefinite (Ignatov and Hedenäs, 2007; Spirina and Ignatov, 2008, 2015; Spirina *et al.*, 2020). Narrow lobes in the front of this image are connected at their bases, proving their homology to the single branch leaf. In the second primordium (Fig. 4D–F) the filamentous tips of the leaf lobes are seen, making possible cell size measurements of their distal parts. The third branch primordium (Fig. 4G) is the least preserved, being near the cut of the amber piece. The lower parts of the proximal branch leaves are hidden in white material, characteristic for the moss parts reaching the amber piece surface (cf. Fig. 1A), but as this view is almost frontal to branch primordium it shows clearly not only outer subfilamentose structures, but also small ovate leaves close to the centre, i.e. the 4th, 5th and 6th leaves of this juvenile branch. The stem leaf subtended this branch primordium in Fig. 4G, is cut and thus its transverse leaf section gives the chance to see cell thickness and additionally measure their width.

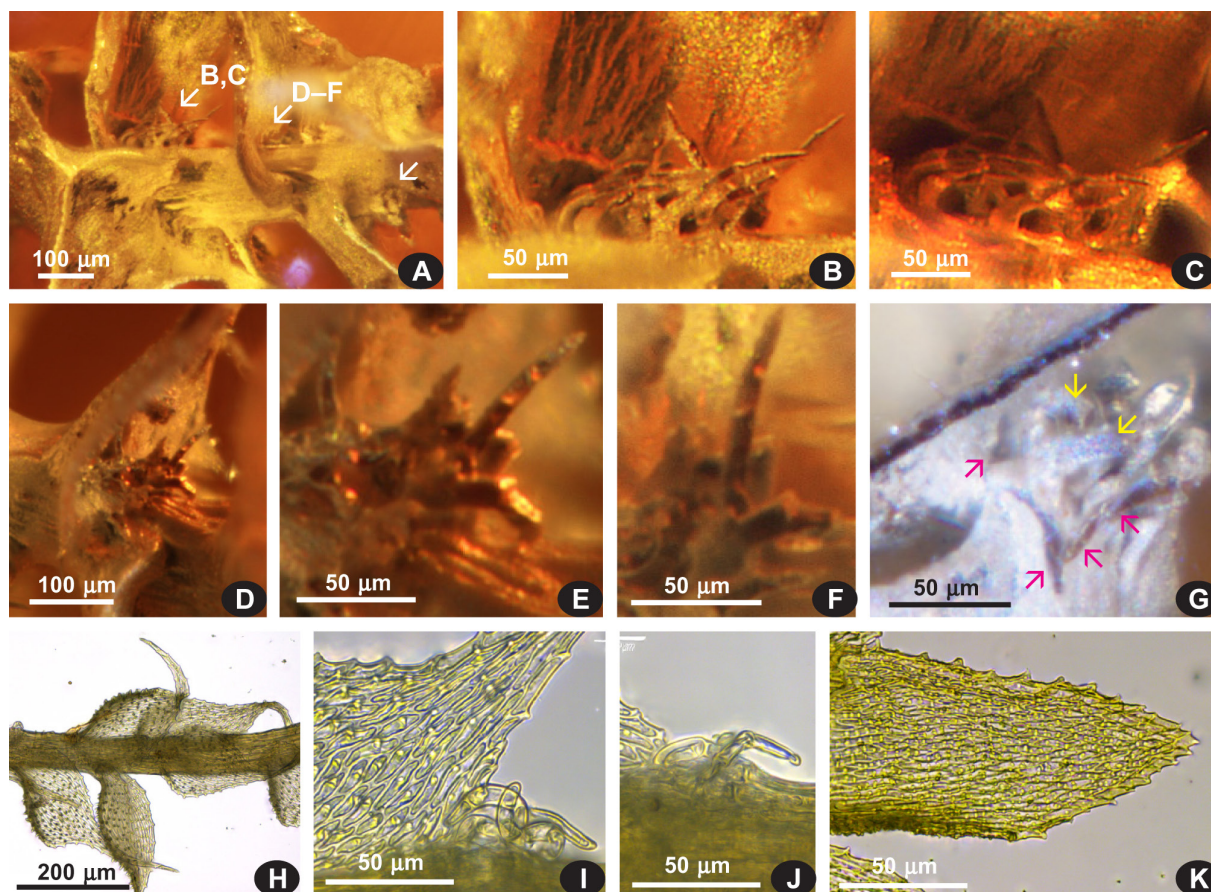


Figure 4. A–G: *Rovnohypnum papillosum* gen. et sp. nov. (from holotype, cf. position of images in Fig. 1A; reflexed light), H–J: *Fauriella tenuis* (from Russian Far East, MHA9004704, transmitted light), K: *Taxitheium kerianum* (from Australia, MHA9058751, transmitted light). A: branch primordia in three leaf axils (arrowed), two of them are magnified in B–F, showing narrow linear and filiform lobes and proximal branch leaves (often called pseudoparaphyllia, but see Spirina *et al.*, 2020). H: part of shoot; I–J: close-ups of H magnifying branch primordia with narrow linear and filiform structures; K: multipapillose cells in front view and as seen in dorsal side on fold due to margin incurvation.

Comparison: The systematic position of *Rovnohypnum* is difficult to find out with confidence. Pleurocarpous habit, attenuate shoot ends, and branch primordia surrounded by foliose structures unequivocally point Hypnales as the order. The familial affinity of *Rovnohypnum* is less apparent. Papillose laminal cells are the common feature of the large family Leskeaceae s.l. (incl. Thuidiaceae), but mosses of this family (often treated as two families) have a stout costa, which is absent in *Rovnohypnum*. *Heterocladium* and *Heterocladia*, the genera previously classified in the Thuidiaceae differ in shorter laminal cells; *Heterocladium* has more concave and catenulate leaves and julaceous shoots. Another family of Hypnales that commonly has multipapillose cells with seriate is Meteoricaceae, but again, a single costa and also ovate proximal branch leaves totally contradict the placement in the latter family.

The habit of *Rovnohypnum* is similar to some small Hylocomiaceae (e.g. *Macrothamnium*) and Lembophyllaceae (*Pseudisothecium*). However, proximal branch leaves in the Hylocomiaceae are ovate, and occasionally only the outermost one, that is situated in five o'clock position, is lanceolate. Lembophyllaceae have branch primordia mostly broad, and even if they are subdivided and incised, they are much broader than in *Rovnohypnum*. Also both these families have usually coarsely serrate leaves and cells are smooth or prorate, never with central position of papilla over cell limina.

Therefore the group of mosses with the short double costa seems to be the most closely related to *Rovnohypnum*: Sematophyllaceae s.l (incl. Sematophyllaceae s. str. and Pylaisiadelphaceae), Pylaisiaceae, Hypnaceae, Pterigynandraceae, and Amblystegiaceae (*Campylophyllum*, *Drepanium*). Many genera of these groups have prorate laminal cells, but only within the Pylaisiadelphaceae and Sematophyllaceae s.str. there are plants with multipapillose laminal cells with seriate papillae, e.g., in the genus *Taxithelium* (Fig. 4K) in Pylaisiadelphaceae, and *Radulina* and *Meiothecium* in Sematophyllaceae s. str., as they are classified by Akiyama (2017) and Akiyama *et al.* (2024). Narrow and distally filiform branch primordia of *Rovnohypnum* (Fig. 4A–G) are subidentical to many genera of Pylaisiadelphaceae, e.g. *Pylaisiadelpha* and *Fauriella* (Fig. 4I, J). Moreover, several genera of the Pylaisiadelphaceae, e.g. in *Clastobryella*, *Brotherella*, and *Aptichella*, and also in fossil genus *Aptichellites*, from the Miocene Caribbean amber (Kaasalainen *et al.*, 2017), have a developed brood filaments in leaf axils of the same length and width as in *Rovnohypnum* (Figs 2C, 3AB).

We do not know any extant genus with the combination of the two traits of *Rovnohypnum*: (1) narrow lanceolate or filiform lobes of proximal branch leaves around branch primordia; (2) papillose laminal cells, with central and sometimes seriate papillae. Therefore we place it in the Pylaisiadelphaceae, as both traits occur in this Pylaisiadelphaceae, but not in other moss families. Putative presence of brood filaments in leaf axils is also supportive, though their interpretation can probably be challenged. *Rovnohypnum* differs from most species of Pylaisiadelphaceae in spreading to somewhat reflexed leaves, while most Pylaisiadelphaceae have more dense foliage, with leaves having a complanate aspect and often being falcate-secund or homomallous. There are some exceptions with terete foliage, e.g. the genus *Fauriella* (Fig. 4H–J), it also has papillose leaves, but with the single papilla per cell. The other papillose species of the Pylaisiadelphaceae may have a variable number of papillae, up to one or none, as in *Taxithelium kerianum* (Broth.) Broth. (Câmara, 2011), shown here in Fig 4K.

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