Arctoa (2025) 34**:** *93–126*
doi: 10.15298/arctoa.34.09

MOSSES FROM THE BYKOVSKY MAMMOTH (YAKUTIA)

МХИ ИЗ БЫКОВСКОГО МАМОНТА (ЯКУТИЯ)

MICHEAL S. IGNATOV[1,2], INNOKENTI S. PAVLOV[3], ELENA I. IVANOVA[4], ELENA A. IGNATOVA[2],
TATYANA V. VORONKOVA[1] & ALBERT V. PROTOPOPOV[3]

МИХАИЛ С. ИГНАТОВ[1,2], ИННОКЕНТИЙ С. ПАВЛОВ[3], ЕЛЕНА И. ИВАНОВА[4],
ЕЛЕНА А. ИГНАТОВА[2], ТАТЬЯНА В. ВОРОНКОВА[1], АЛЬБЕРТ В. ПРОТОПОПОВ[3]

Abstract

Moss collection of the Late Pleistocene, 48850±2274 years old, from in the Neelov Bay of the Laptev Sea, Arctic Ocean was obtained from the mammoth scull, within the nose cavity. Mosses are preserved in excellent condition since the Bykovsky Mammoth has been fossilised shortly after its death, buried in permafrost ground and never melted until its finding in 2022. Bulk maceration of soil with mosses brought about 500 moss fragments; 135 better preserved specimens were mounted in slides. Thirty two species were identified up to species level, whereas one small fragment of *Sphagnum* and two leaves of *Didymodon* were referred only to the genus. Species composition of this collection is generally similar to that currently occurring in the area; the collection includes mire species *Scorpidium scorpioides, Loeskypnum badium, Calliergon richardsonii, Drepanocladus brevifolius, D. trifarius*, *Tomentypnum involutum*, *Meesia uluginosa, Orthothecium chryseon*, as well as epigeic mosses *Encalypta alpina*, *E. procera*, *Tortella splendida, Distichium capillaceum, Flexitrichum flexicaule,* and *Abietinella abietina*. Northern flora element is represented by *Cyrtomnium hymenophyllum* and *Polytrichastrum septentrionale*. Among mosses with more southern distribution we found *Leskea polycarpa*, a species having its northern limit in Lower Lena River region at ca. 300 km to the south. The latter fact provides an evidence, in addition to the scattered paleoclimatological data, that in time when Bykovsky Mammoth lived the northern Yakutian climate was slightly warmer than now, unlike the climate of Europe, where it was colder that time.

Резюме

Образцы мхов позднеплейстоценового возраста, 48850±2274 лет, были найдены в носовой полости черепа мамонта, который был обнаружен на берегу залива Неёлова в море Лаптевых. Мхи имели отличную сохранность благодаря тому, что этот Быковский мамонт оказался фоссилизированным вскоре после своей смерти, будучи захороненным в мерзлом грунте и не оттаивая вплоть до его нахождения в 2022 году. Объемное мацерирование почвы с вкраплениями мхов позволило получить около 500 фрагментов мхов; 135 из них, лучше сохранившиеся, были заделаны в постоянные препараты. Было определено 32 мха до уровня вида, а один фрагмент сфагнума и два листа *Didymodon* можно было определить только до рода. Видовой состав изученной коллекции оказался сходным с видовым составом мхов, произрастающих в этом районе в настоящее время; в ней были найдены болотные виды *Scorpidium scorpioides, Loeskypnum badium, Calliergon richardsonii, Drepanocladus brevifolius, D. trifarius*, *Tomentypnum involutum*, *Meesia uluginosa, Orthothecium chryseon*, а также наземные мхи *Encalypta alpina*, *E. procera*, *Tortella splendida, Distichium capillaceum, Flexitrichum flexicaule* и *Abietinella abietina*. Северный флористический элемент представлен такими видами, как *Cyrtomnium hymenophyllum* и *Polytrichastrum septentrionale*. Из видов с более южным распространением следует отметить *Leskea polycarpa*, северная граница распространения которой в нижнем течении р. Лена проходит на 300 км южнее. Этот факт является дополнительным свидетельством в пользу того, что на севере Якутии в позднем плейстоцене было немного теплее, чем сейчас, в отличие от Европы, где климат в те времена был холоднее, чем в настоящее время.

KEYWORDS: Late Pleistocene, bulk maceration, fossil mosses, mire moss species

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[1] – Tsitsin Main Botanical Garden, Russian Academy of Sciences, Botanicheskaya Str., 4, Moscow 127276 Russia. E-mail: misha_ignatov@list.ru; ORCID: (MI) 0000-0001-6096-6315; (TV) 0000-0002-6112-271X

[2] – Lomonosov Moscow State University, Faculty of Biology, Plant Ecology and Geography Dept., Leninskie Gory Str. 1–12, Moscow 119234 Russia. E-mails: arctoa@list.ru; (EI) 0000-0001-6287-5660

[3] – Academy of Sciences of Republic of Sakha (Yakutia), 33 Lenina pr., Yakutsk, 677007, Russia. E-mail: a.protopopov@mail.ru ORCID: (IP) 0000-0002-4417-1800; (AP) 0000-0001-6543-4596.

[4] – Institute for Biological Problems of Cryolithozone of Siberian Division of Russian Academy of Sciences, 41 Lenin ave., Yakutsk, 677000, Russia. E-mail: bryo.ivanova@yandex.ru ORCID: 0000-0002-0387-9810.

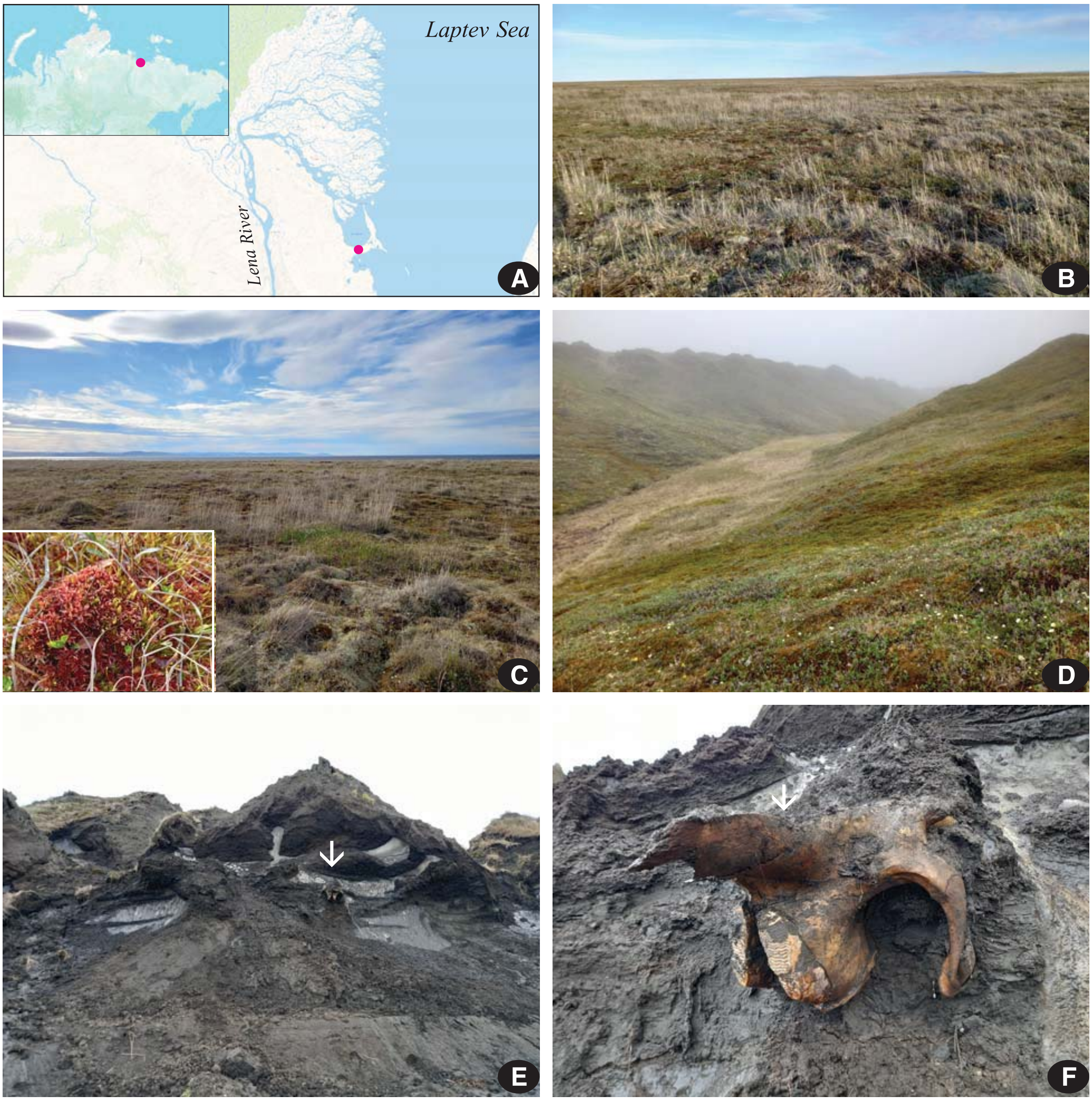


Fig. 1. Bykovsky Mammoth locality (A, red dot on maps); current tundra vegetation, dominated by mosses, lichens and *Festuca brachyphylla* Schult. & Shult, *Poa arctica* R.Br., and sedges *Carex bigelowii* subsp. *arctsibirica* (Jurtz.) A. & D. Love (B), at places with the permafrost hummocks (C), forming a wetter environment suitable for *Sphangum* cf. *capillifolium* and *Aulacomnium turgidum* (C, inset); a brook valley, with dwarf shrubs of *Salix arctica* Pall., *Salix reptans* Rupr. (D), with *Dryas incisa* Juz. and *Dryas punctata* Juz. (D, white flowers). E: mammoth scull on the slope with melting permafrost (arrowed); D: mammoth scull, showing the place of nose cavity, where mosses buried in soil were collected (arrowed).

INTRODUCTION

The Late Pleistocene is characterised by global changes in ecosystems which resulted, among others, in a mass extinction of large mammals in Northern Eurasia. Yakutia is especially rich in findings of *Mammuthus primigenius* Blumenbach, 1799, a long-hair northern relative of Indian elephants (*Elephas maximus indicus*). The extensive permafrost in Yakutia, reaching at places over 1000 m deep serves as a giant freezer, preserving living beings in excellent state. Plants retain their structure, and in the exceptional case of *Silene stenophylla,* seeds of 32 Kyr old were propagated, developed mature plants and even bloomed (Yashina *et al*., 2012).

Previous plants records from the permafrost of Yakytia helped to restore the history of the last period of the ice age in considerable details (Protopopov, 2017). Important data were also provided by Tomskaya (2000) and Ukraintseva (2002), who found in the Pleistocene animal gastrointestinal tracts many plant remnants. In five cases they saw bryophytes, which occasionally constituted as much as 27% of the stomach content, but usually they were almost impossible to identify. The largest list of Plestocene

Fig. 2. A: mosses after bulk maceration treatment; B: *Sphagnum* sp. (#7_1).

mosses in Northern Asia has been published by Abramov & Abramova (1981). It includes 44 species (including identifications up to genus), from the soil and debris surrounding the Kirgilyakh Mammoth from the upper course of Kolyma River in Magadan Province, dated for 41000±900 years old (Ukraintseva, 2002).

Nonetheless, rich plant collections in fossil animals are still few and often have a limited value because the stomach content is usually partly digested. We present here an expanded description of a moss collection found within the mammoth scull. It remains unclear how exactly these mosses appeared in it, but it is apparent that it happened shortly before its burial in frozen soil.

MATERIAL AND METHODS

Bykovsky Mammoth has been discovered by the join expedition of the Academy of Sciences of the Republic Sakha (Yakutia) in 2022. The locality (Fig. 1A) is in the Bykovsky Peninsula, shore of Neyolov Bay of Laptev Sea, ca. 3 km N from the Kolychev Isthmus (Kandyba *et al*., 2022). Now the area is covered mostly by flat tundra vegetation (Fig. 1B), occasionally with small lakes, wet depressions with *Eriophorum callitrix* Cham. ex C.A. Mey and *E. vaginatum* L., in wetter places with permafrost hummocks (Fig. 1C), and ravines with small brooks (Fig. 1D). Mosses, lichens and small grasses prevail, and shrub communities of dwarf *Salix arctica* and *S. reptans* have a limited distribution in wet sites, especially in ravines.

AMS radiocarbon dating of the mammoth found its age 48850±2274 years, GV-4954 (identifyed in the Novosibirsk State University and in the Institute of the automatics and electrometry).

The mammoth bones were found mostly within the ice on slope to the Neyolov Bay, in its hilly part, at 7 to 12 m above sea level and at the depth of 24 m below the daylight surface (1E, F). The mammoth skeleton was incomplete, representing about 20% of bones of a young mammoth, apparently 15–20 years old. Traces of damage on bones indicate that it was likely killed and then eaten by ancient men (Kandyba *et al*., 2022).

In addition to mammoth bones, cartilaginous tissue on bone joints and a part of stomach with perfectly preserved remnants of plant food were found. These plant remnants provide an evidence not only for that the mammoth was frozen and buried shortly after its death, but also indicate that it apparently happened in the late summer of early autumn, as *Carex* fruits in the stomach had mature seeds. These aspects of preservation of the Bykovsky mammoth prove that it never melted since it was buried, so its soft tissues could partly remain.

Bryophytes in mammoth scull were found within soil that filled the nose cavity (Fig. 1F), while temporal cavities near eye pits were filled by shrub twigs and grasses. Soil from the nose cavity was sifted through the sieve with 8 mm meshes, and pieces were sorted for bryophytes, vascular plants, and insects. Some vascular plant fragments (e.g., the *Carex* perigynia, small grass fragments) were found as an admixture to mosses. The sample ca. 100 g with mosses was delivered to Tsitsin Main Botanical Garden Herbarium for moss identification.

Bryophytes preparation by a simple washing appeared to be not appropriate, because moss fragments were fragile and also because the standard washing still leaved too much dirt precluding detailed examination. Therefore, we applied a bulk maceration method, which is commonly used for the study of Paleozoic fossils (Ignatov *et al*., 2023, 2024).

The pieces of soil with mosses were originally put in ethylene diamine tetraacetic acid disodium salt (EDTA) solution for the calcium carbonate chelating; after three days, the hydrofluoric acid has been added. After two weeks, the main part of soil has been dissolved leaving moss remnants clean and ready for mounting in slides, though some samples still looked somewhat dirty (apparently due to remaining of pyrite and other highly resistant compounds). This dirt, however, did not preclude plant studies sufficiently, and after multiply washing for complete removal of HF acid we started moss studies (Fig. 2A).

The best samples in the obtained material looked almost like just collected extant mosses, and it was possible to use them for sectioning with razor blade. Other moss remnants were partly decayed, so they could not be cut, and even an attempt to detach a leaf from the stem can not always be successful, as even a light touch with forceps broke the leaf.

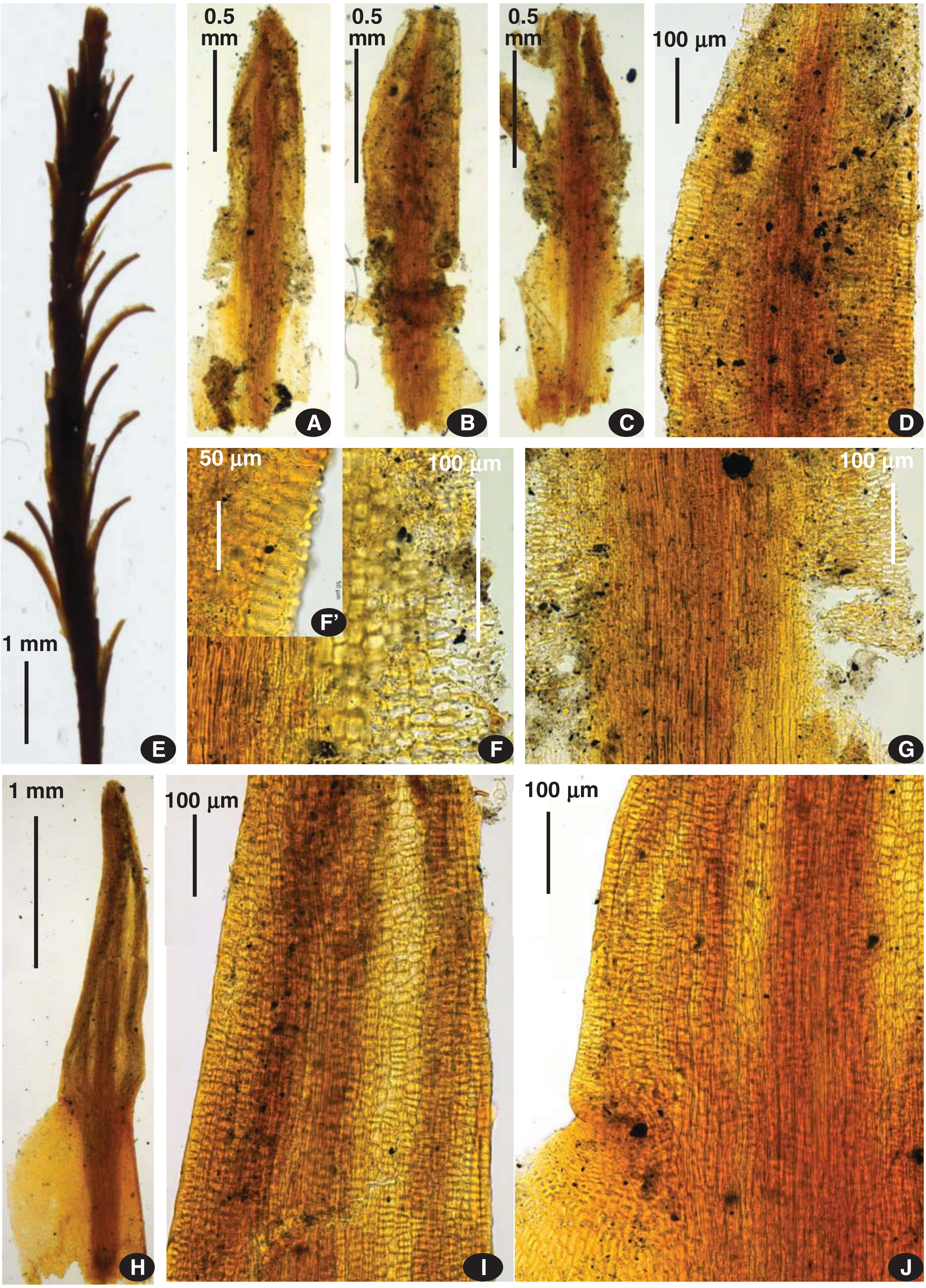


Fig. 3. *Polytrichum strictum*. A: leaf (5_4B_1); B: leaf (5_4B_3); C: leaf (5_4B_2); D: mid-leaf cells, ventral view (5_4B_3); E: shoot; F: mid-leaf cells, ventral view (5_4B_1); G: mid-leaf cells, dorsal view (5_4B_1); H: leaf (#5_2B_3); I: upper leaf cells (#5_2B_3); J: cells at the transition from leaf base to blade (#5_2B_3).

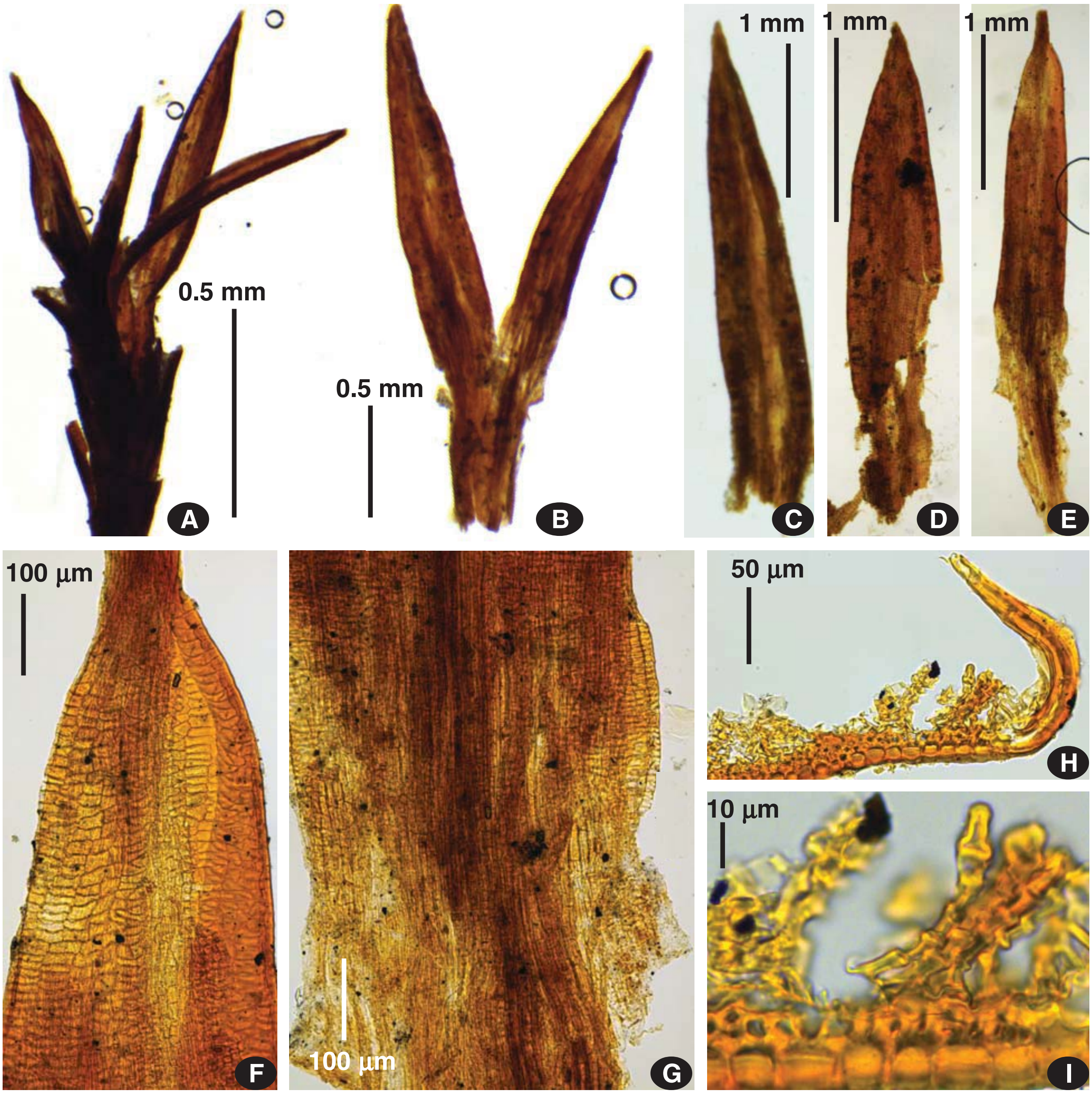


Fig. 4. *Polytrichum* cf. *juniperinum*. A–B: shoots; C: leaf; D: leaf (#2_3A_2), E: leaf (#2_3A_1); F: upper leaf cells, ventral view (#2_3A_1); G: cells at the transition from leaf base to blade (#2_3A_2); H–I: leaf transverse sections showing ventral lamellae with flask-shaped apical cells (#2_3B_3).

First, we selected the better preserved shoots and photographed them with stereomicroscope Nikon SMZ-25 in water in Petri dishes. Then some their leaves were detached and stems and leaves were sectioned when needed, and all obtained fragments from one shoot were mounted to one permanent slide with glycerol jelly. Second, best dispersed leaves were mounted to permanent slides. Third, poorly preserved samples but representing taxa putatively not yet selected, were prepared for additional slides with double care minimising distructive actions.

Then specimens were photographed under the Olympus CX43 light microscope with the Infinity 1–2 camera. Z-stacks of several images were generated using Helicon-Focus 4.50 (Kozub *et al*., 2008).

Description of specimens addresses mostly to the traits that are useful for the species identification in nature and also in the peat drill studies. As a reference, the "Moss flora of Russia" was used (Ignatov *et al*., 2017, 2018, 2029, 2022, 2025).

RESULTS

Sphagnum **sp.** (Fig. 2B). Only one small fragment of leaf with characteristic for *Sphagnum* cell areolation was found in the studied material. It likely belongs to stem leaf because its hyaline cells lack fibrils. However, it is impossible to name even subgenus, let alone a species.

Polytrichum strictum Menzies ex Brid. (Fig. 3). We refer to this species a shoot ca. 10 mm long with partially decomposed leaves having appressed leaf bases and

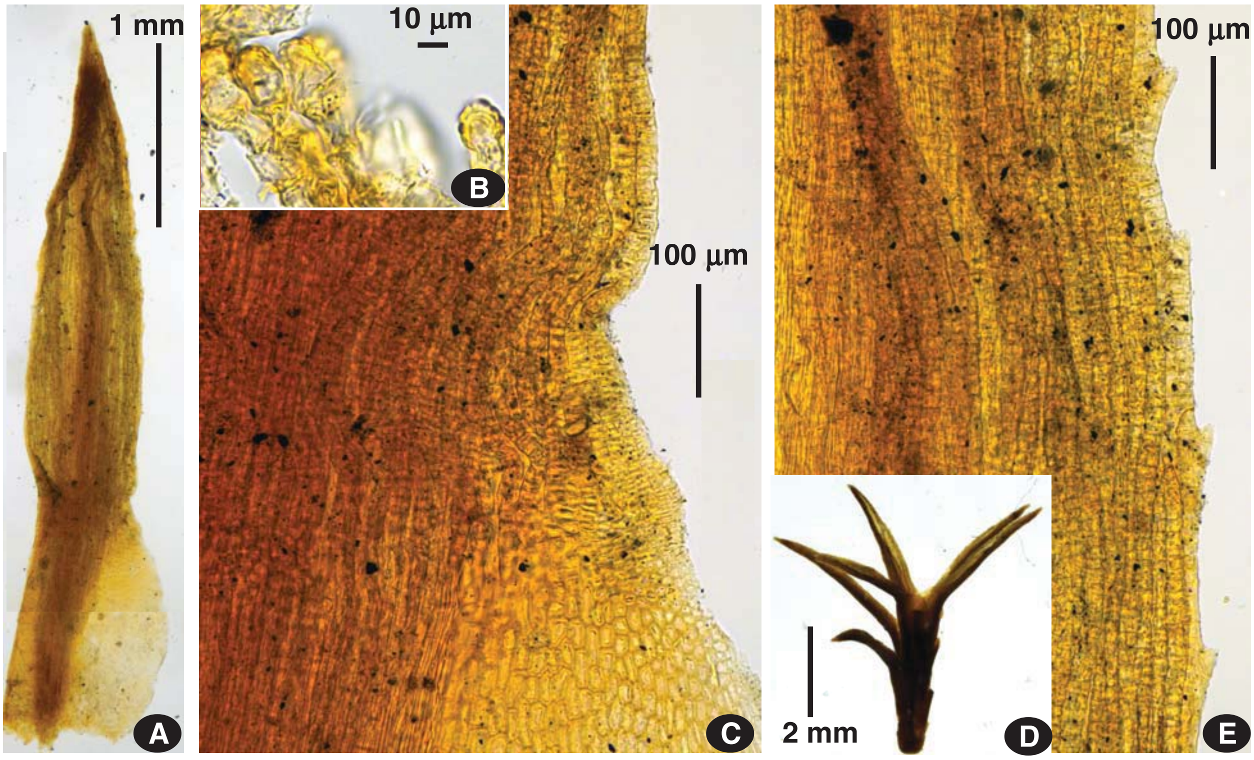


Fig. 5. *Polytrichastrum alpinum*. A: leaf (#5_2B_1); B: papillose apical cells of ventral lamellae in transvere section (#5_2B_2); C: cells at the transition from leaf base to blade (#5_2B_1); D: shoot; E: cells at the blade margin (#5_2B_1).

erectopatent remnants of blades (Fig. 3E). Three partially destroyed leaves, 2.2–2.4×0.7–0.9 mm, were removed from this shoot (Figs. 3A–C); one similar intact leaf 3.3×1.1 mm with widely incurved, entire leaf margins was found separately (Fig. 3H). In these leaves, costa occupies ca. 1/3 the width of blade, and ventral lamellae can be guessed as longitudinal striae on the costa surface. The inflexed upper leaf margins are formed by oblate, transparent cells in 6–8 rows, better seen in Figs. 3F–G, I–J. This character is shared by *P. strictum* and *P. juniperinum*; furthermore, these two species are occasionally considered as merely ecological forms, possessing intermediate expressions (Ivanova & Ignatov, 2017). We attribute this plant to *P. strictum* despite its leaves are not tightly appressed to the stem because it is tall and evenly foliate, with twelve leaves apparently of the same size.

Polytrichum cf. ***juniperinum*** Hedw. (Fig. 4). This species is represented by a shoot ca. 2.5 mm long with four intact leaves and several leaf bases with broken off blades (Fig. 4A), a fragment of stem with two intact leaves (Fig. 4B), and three leaves (Fig. 4C–E). The latter leaves are 2.7–3.3×0.5–0.8 mm, they have intact blades and partly decomposed bases. One leaf was transversely sectioned, showing inflexed leaf margins (Fig. 4H) and ventral lamellae with pyriform, smooth apical cells (Fig. 4I). Inflexed leaf margins composed of oblate cells are observed (Fig. 4F), and vertical striae on costa in Fig. 4G indicate presence of ventral lamellae. In leaf structure this plant is very similar to *P. strictum*, but we tentatively attribute it to *P. juniperinum* due to a shorter stem with fewer leaves.

Polytrichastrum alpinum (Hedw.) G.L. Sm. (Fig. 5). A shoot ca. 3 mm long (Fig. 5D) with six leaves having erectopatent blades apparently belongs to the genus *Polytrichastrum* due to its leaf margins with small teeth formed by more than one cell (Fig. 5E). One leaf was removed from this shoot; it is 3.9×1 mm in size, its blade has flat margins with small, distant, 2–3-celled teeth; there is also a constriction between its blade and leaf base (Fig. 5A). A transverse section was obtained from another leaf from this shoot; it possesses distalmost cells of ventral lamellae with stronger thickened distal wall and massive round papillae (Fig. 5B). The latter character suggests that this plant may belong either to *P. alpinum* or *P. fragile*. However, the latter species commonly has at least some leaves fallen off due to fragility, and also its blade margins are entire or weaker toothed, while in this specimen leaves are toothed as in *P. alpinum*.

Polytrichastrum septentrionale (Sw. ex Brid.) E.I. Ivanova, N.E. Bell & Ignatov (Fig. 6). We attribute to this species two shoots 5–10 mm long: one with one intact and tree partially broken leaves (Fig. 6A) and another with three intact and three partially broken leaves (Fig. 6B). One leaf with intact blade and partially broken base 4×1.2 mm (Fig. 6C) has a narrow triangular blade with flat margins and abruptly widened base. Blade marginal teeth are composed of 2–3 cells (Fig. 6E). Leaf transverse section shows ventral lamellae 4–6 cells high and distalmost cells with strongly thickened, finely papillose distal wall. This character combination makes identification of the plant confident.

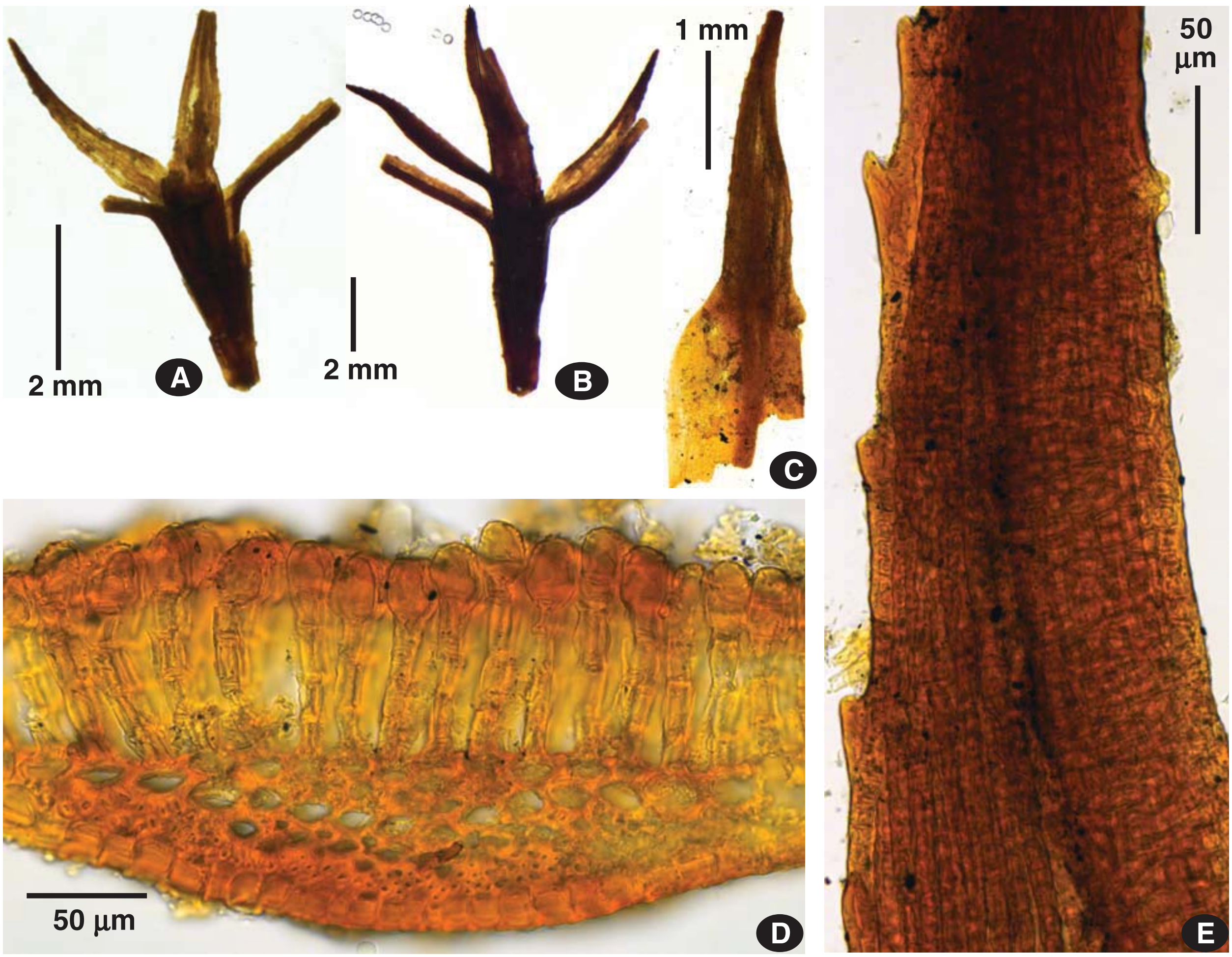


Fig. 6. *Polytrichastrum septentrionale*. A–B: shoots; C: leaf (#1_1_1); D: leaf transvere section (#1_1_2); E: cells at blade margin (#1_1_1).

Encalypta procera Bruch (Fig. 7) is represented by a small shoot ca. 5 mm long (Fig. 7A) with 10 leaves, most of which are erect, crowded at stem top, and one leaf is arcuate-spreading. Three leaves removed from this shoot are shown in Figs. 7B–D; they are lingulate, 3.2×0.95 mm, 3.4×0.7 mm, and 3.6×0.9 mm, with obtuse or widely acute apices, margins plane distally and narrowly recurved in basal 1/3–1/2; costae are percurrent, gradually narrowing distally. Distal laminal cells are isodiametric, quadrate or polygonal, 16–19 μm in diameter, papillose, papillae moderately dense, C-shaped (Figs. 7 G, I). They are gradually transiting into rectangular, smooth basal cells (Fig. 7F). Basal laminal cells are mainly destroyed (Fig. 7E), but it is seen at places that they have thin longitudinal and thick, light-brownish transverse walls (Fig. 7H). This combination of characters allows us to refer this plant to the genus *Encalypta* with confidence. It is also most likely that it can be named *E. procera* due to its large, obtuse leaves with percurrent costa and, especially, mainly destroyed basal laminal cells which is apparently caused by the development of brood filaments in leaf axils (though not found in this fossil shoot).

Encalypta alpina Sm. (Fig. 8). Three shoots of this species were found in the studied material; one of them, 4.3 mm long, with six intact leaves and three partly broken ones, is shown in Fig. 8A. Two larger leaves from this shoot are 2.6 ×0.7 mm and 2.8×0.7 mm; three leaves are smaller, 1.6–1.7×0.5–0.7 mm. All leaves are oblong-ovate to lanceolate, with acute apices and short-excurrent costae. Densely papillose upper laminal cells (Fig. 8I, J, L) and partly destroyed, smooth basal cells with stronger thickened transverse walls (Fig. 8K) make referring this specimen to the genus *Encalypta* straightforward. Its species identification is also easy due to acute leaf apices (Fig. 8I, L).

Distichium capillaceum (Hedw.) Bruch & Schimp. (Fig. 9). Two shoots of this species 4.7 mm long are shown in Figs. 9A, C. One of them has most leaves with intact laminae, while in the second one leaves are partly broken. Their placement into the genus *Distichium* is unmistakable due to clearly distichous leaf arrangement and leaf shape, with ovate bases clasping the stem and subulate, patent laminae. Cell areolation at leaf shoulders is seen on small stem fragment 1.5 mm long with few leaves: cells are transiting from short rectangular to quadrate, they are smooth. Species identification is, however, impossible without sporophytes, since capsule shape and spore size possess species distinctions. We tentatively refer these plants to *D. capillaceum*, the commonest species of the genus occurring in North Asia.

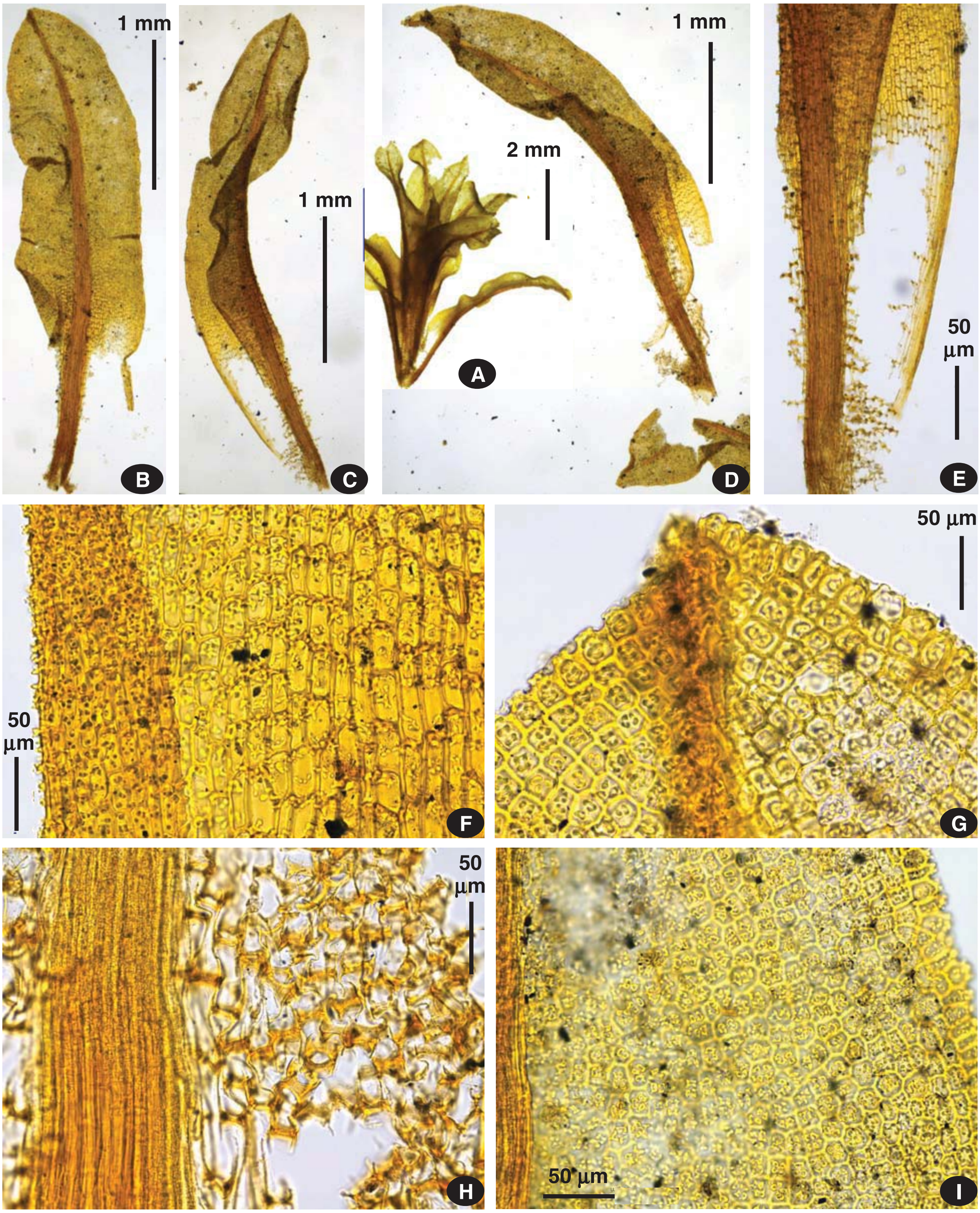


Fig. 7. *Encalypta procera*. A: shoot; B: leaf (#5_3B_1); C: leaf (#5_3B_3); D: leaf (#5_3B_2); E: leaf base (#5_3B_3); F: cells shortly above leaf base (#5_3B_4); G: upper leaf cells (#5_3B_1); H: cells of pellucid part of leaf base, showing incrassate transverse walls (#5_3B_3); I: multipapillose upper leaf cells (#5_3B_1).

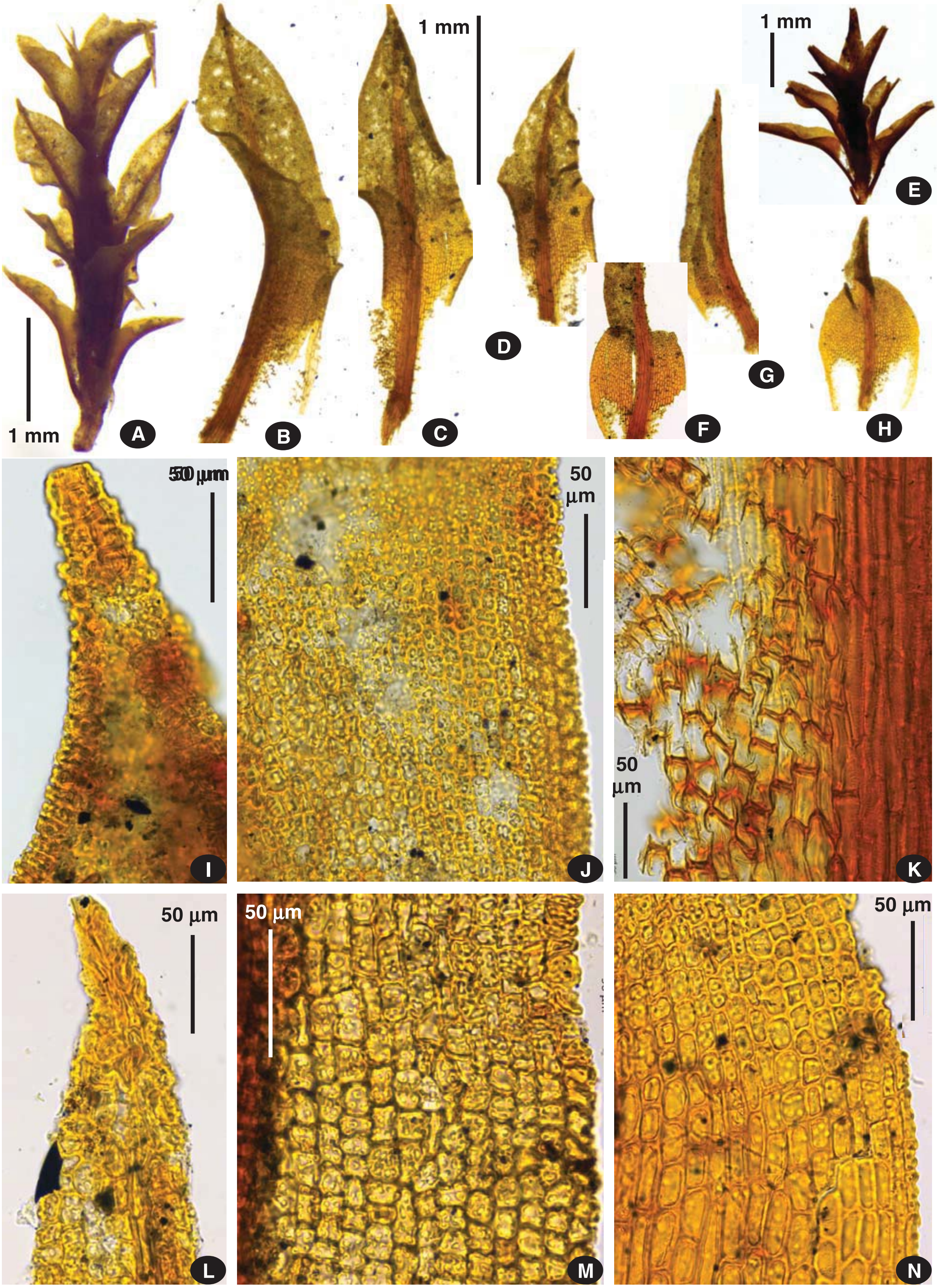


Fig. 8. *Encalypta alpina*. A, E: shoots; B: leaf (#3_4B_1); C: leaf (#3_4B_2); D: leaf (#3_4B_3), F: leaf (#1_2A_1); G: leaf (#1_2A_2); H: leaf (#3_4B_4); I: upper leaf cells (#3_4B_2); J: mediam leaf cells (#3_4B_2); K: basal leaf cells (#3_4B_2); L: upper leaf cells (#1_2A_2); M: mediam leaf cells (#1_2A_2); N: cells shortly above leaf base (#1_2A_1).

Fig. 9. *Distichium capillaceum*. A: shoot (#1_2B_1); B: shoot (#1_2B_3); C: shoot; D: cells at leaf shoulder (#1_2B_3).

Flexitrichum flexicaule (Schwägr.) Ignatov & Fedosov (Fig. 10). This species is represented by a shoot 1.3 mm long (Fig. 10a) with erectopatent leaves, mostly with broken upper parts; however, three leaves are almost intact, possessing long, subulate acumina. Two leaves from this shoot with broken off tips are 2.1×0.35 mm and 1.7 ×0.3 mm, from ovate bases ±abruptly narrowed into long acumina, with shoulders (Fig. 10F, G). Costa occupies 0.6–0.8 of the width of acumina (Fig. 10B, C); upper lamina cells are subquadrate. This plant can be referred to the genus *Flexitrichum* with confidence due to narrow, thin-walled cells with oblique transverse walls in 2–3 marginal rows just below the shoulders (Fig. 10D, E). Short rectangular, eporose basal juxtacostal cells (Fig. 10D) prove its species identification as *F. flexicaule*.

Fissidens adianthoides Hedw. (Fig. 11). Two remnants of *Fissidens* were found in the studied material: one shoot fragment 1.9×2.1 mm with five leaves (Fig. 11A) and one entire leaf (Fig. 11B) 2.2×0.9 mm, with acute apex and percurrent costa. This leaf apparently belongs to *F. adianthoides* due to its shape and size, lack of marginal border of linear cells but presence of indistinct border of 2–3 rows of thicker-walled cells (Fig. 11C, E), and distant teeth at margins below the apex (Fig. 11C). Upper and median laminal cells are round-hexagonal, ca. 20 µm in diameter, which also agrees with the description of *F. adianthoides*. Its dorsal lamina is gradually narrowing to the insertion and shortly decurrent (Fig. 11G). However, identification of the shoot fragment is less straightforward: tips of its leaves are broken off, so it is unknown if they are acute, where the costa ends, are their upper margins dentate or not, and it is not seen if their dorsal laminae are decurrent or rounded to the insertion. Another species with unbordered margins is *F. osmundoides*. However, we consider that this fragment also belongs to *F. adianthoides* because it was found in close proximity to the single leaf, and its leaves and cells have the same size as the latter leaf.

Didymodon cf. ***borealis*** Ignatova & Ignatov (Fig. 12). We attribute tentatively to this species a shoot 2.7 mm long with partially broken, erect-spreading leaves. Two almost entire leaves detached from this shoot are shown in Fig. 12B. They are both ca. 0.97×0.3 mm, gradually tapering from ovate bases into narrow triangular acumina, with thin, percurrent costa and weakly recurved margins below midleaf. Upper and mid-leaf laminal cells are subquadrate, smooth; basal juxtacostal cells are short rectangular. This combination of characters fits best a recently described species *D. borealis*, which presently occurs in Yakutia and Anabar Plateau.

Fig. 10. *Flexitrichum flexicaule*. A: shoot; B: upper leaf cells (#3_6B_2); C: upper leaf cells (#3_6B_1); D: cells at leaf shoulder showing marginal cells with oblique walls (#3_6B_3); E: cells at leaf shoulder showing marginal cells with oblique walls (#3_6B_1); F: leaf (#3_6B_1); G: leaf (#3_6B_2).

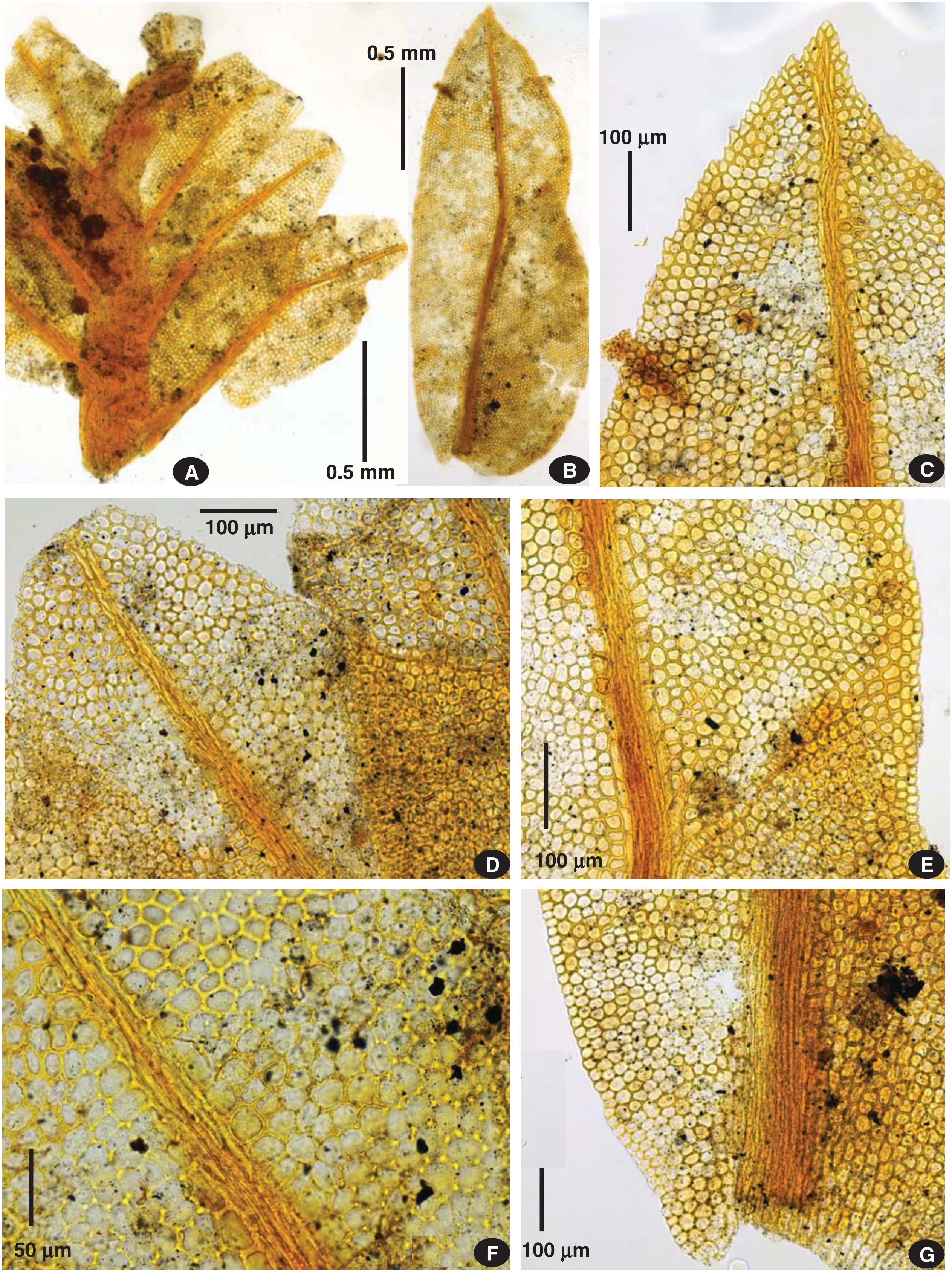


Fig. 11. *Fissidens adianthoides*. A: shoot (#2_4B_1); B: leaf (#2_4A_1); C: upper leaf cells (#2_4A_1); D: ipper leaf cells (#2_4B_1), F: upper leaf cells (#2_4B_1); E: cells at place of attachment of smaller vaginant lamina (#2_4A_1); G: basal cells of dorsal and vaginant laminae (#2_4A_1).

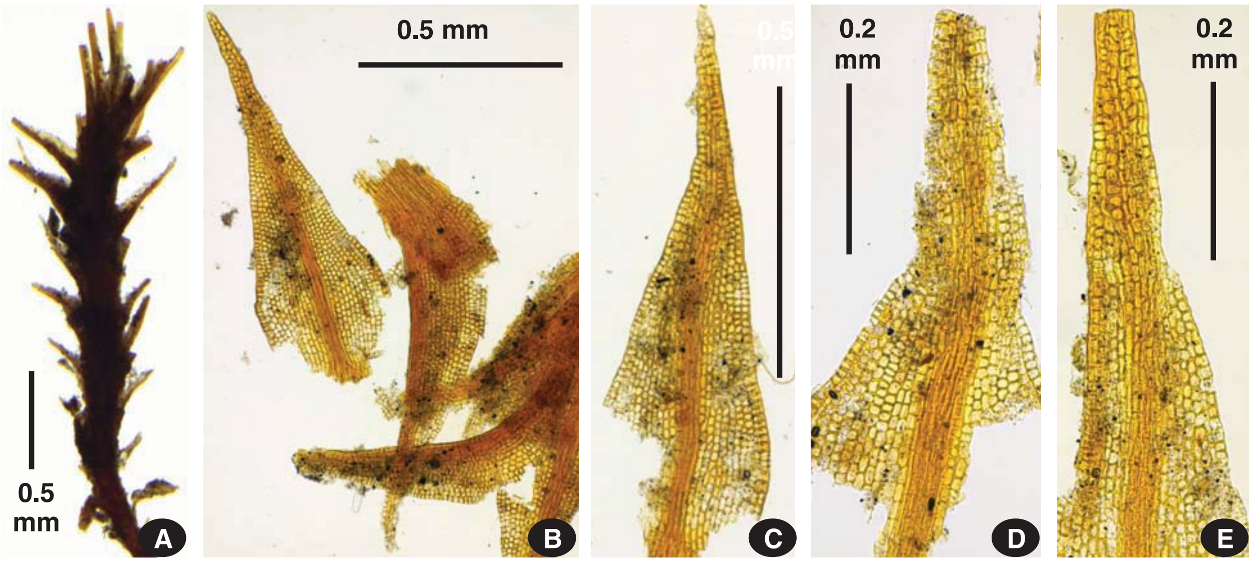


Fig. 12. *Didymodon* cf. *borealis*. A: shoot; B: leaves (#1_2B_2); C: leaf (#1_2B_4); D: mid-leaf cells (#1_2B_5); E: mid-leaf cells (#1_2B_6).

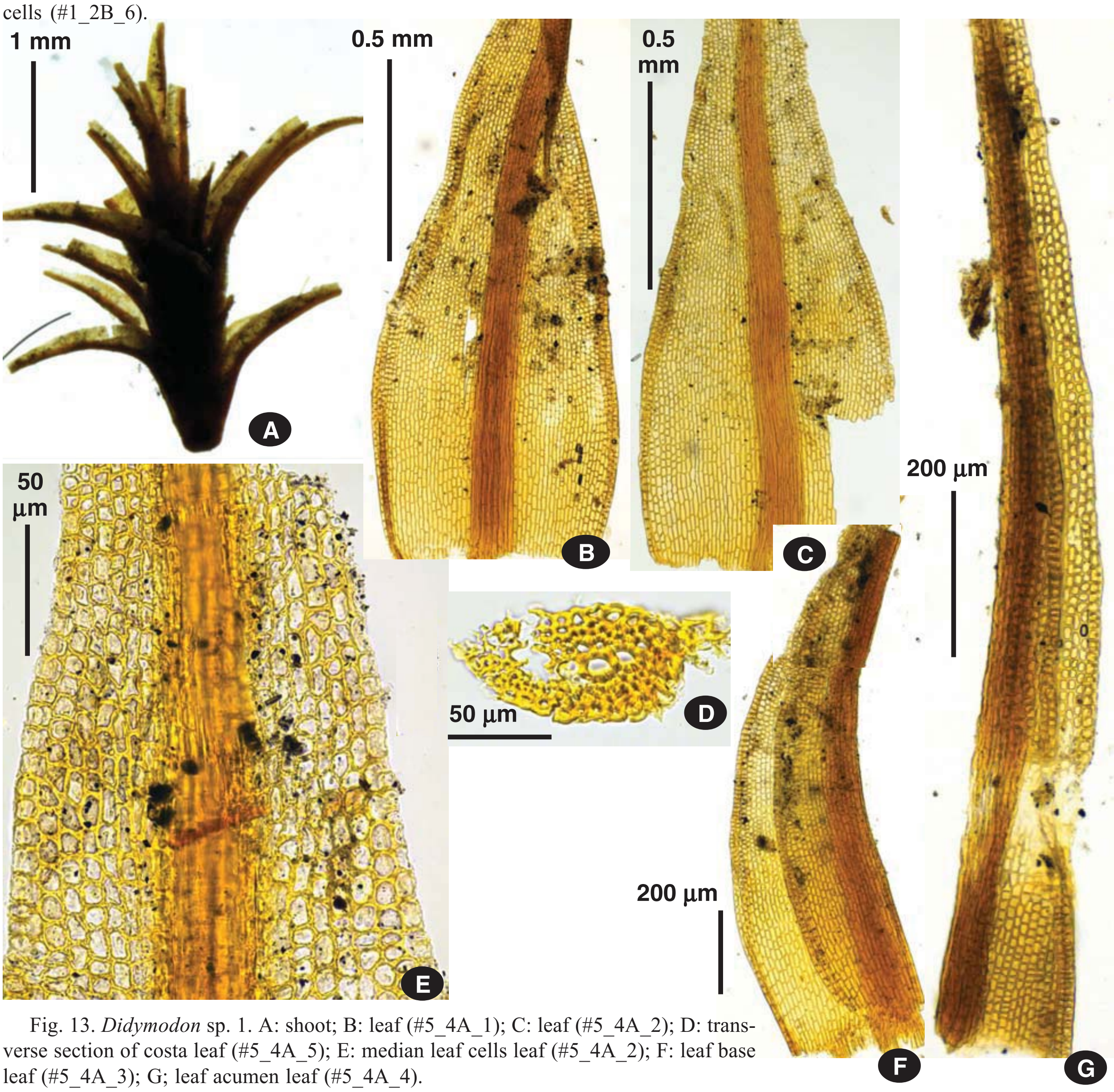


Fig. 13. *Didymodon* sp. 1. A: shoot; B: leaf (#5_4A_1); C: leaf (#5_4A_2); D: transverse section of costa leaf (#5_4A_5); E: median leaf cells leaf (#5_4A_2); F: leaf base leaf (#5_4A_3); G; leaf acumen leaf (#5_4A_4).

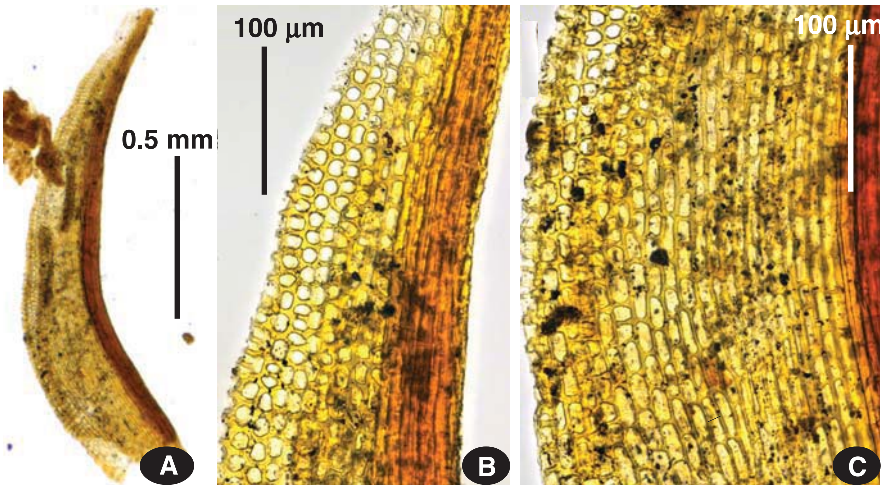


Fig. 14. *Didymodon* sp. 2 (#6_1A_1 for all). A: leaf; B: upper leaf cells; C: basal laminal cells.

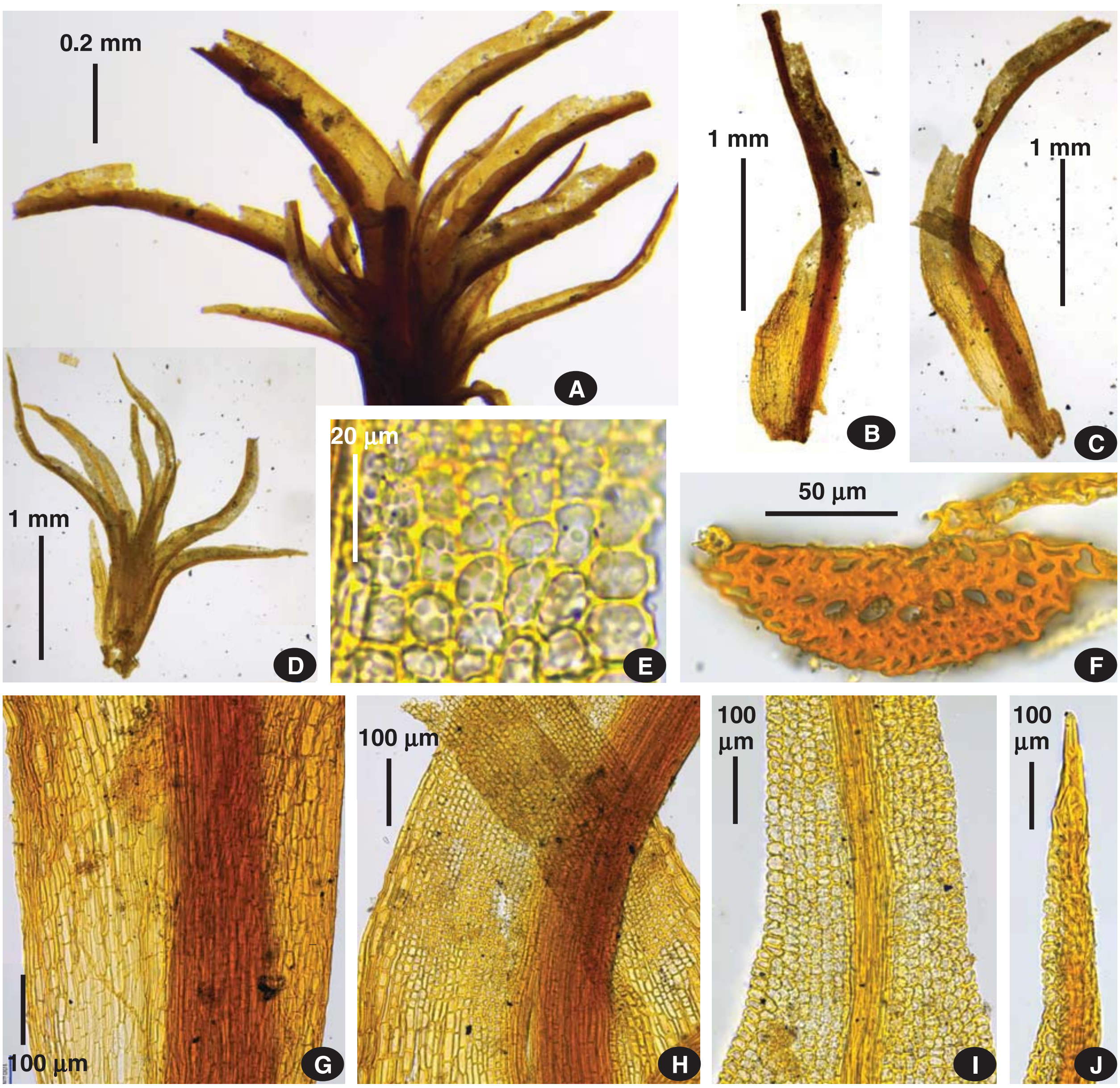


Fig. 15. *Tortella splendida*. A: shoot; B: leaf (#3_6A_3); C: leaf (#3_6A_2); D: shoot (#3_6A_1); E: upper leaf cells (#3_6A_1); F: transverse section of costa (#3_6A_4); G: basal leaf cells (#3_6A_2); H: transition from basal to median laminal cells (#3_6A_2); I: upper leaf cells (#3_6A_1); J: uppermost leaf cells (#3_6A_1).

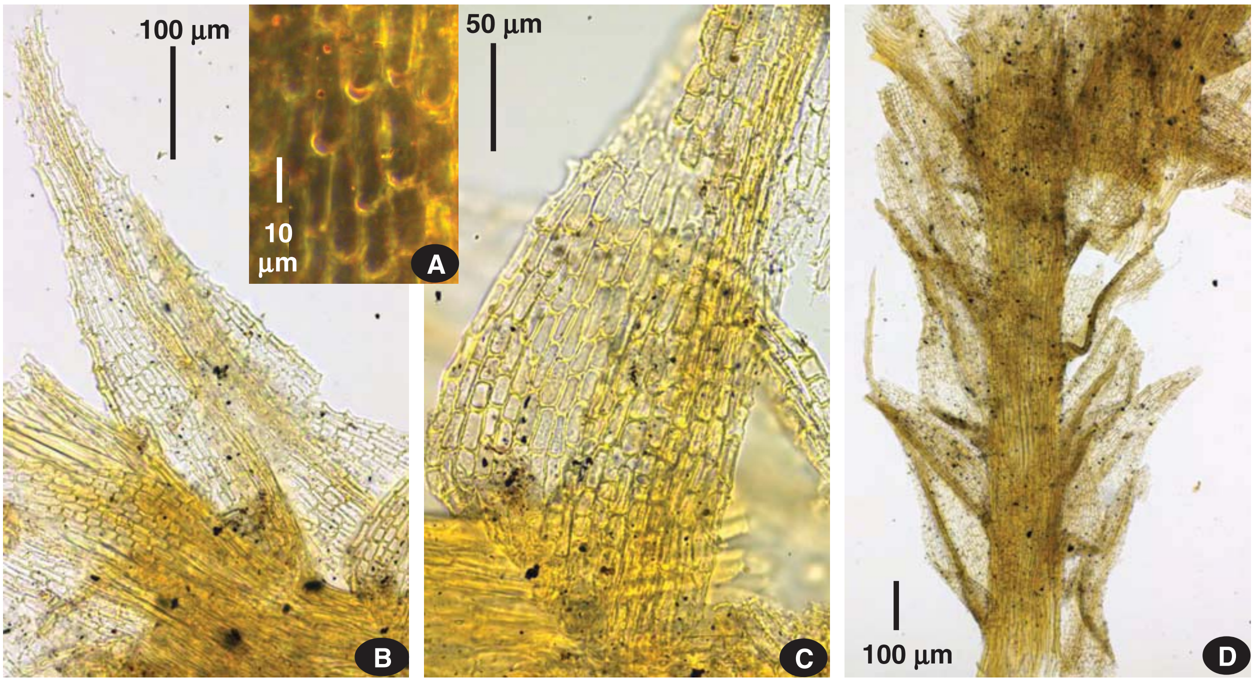


Fig. 16. *Philonotis tomentella* (#16_1_1 for all). A: basal laminal cells (darkfield condenser image); B: leaf; C: leaf base; D: shoot.

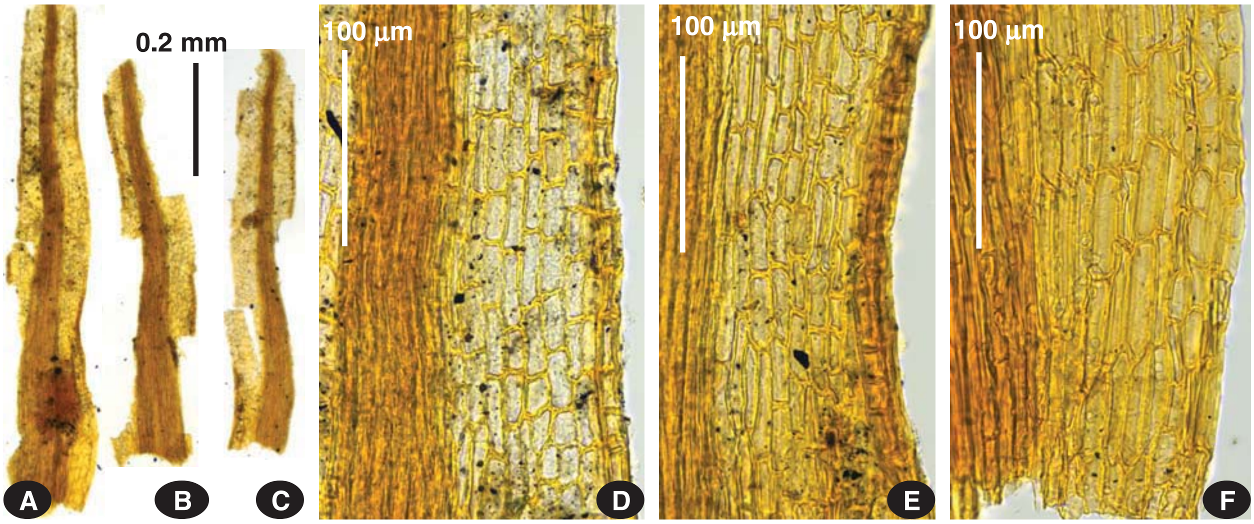
Didymodon sp. 1 (Fig. 13). One shoot 3.4 mm long with spreading, partially broken leaves (Fig. 13A) represents another species of *Didymodon*. Its leaves are apparently longer than 2 mm; two leaf fragments (their basal parts) are 1.3×0.6 mm (Fig 13B–C) and a part of narrow acumen is 1.2 mm long (Fig. 13G). Their size and shape together with subquadrate, smooth upper laminal cells and short rectangular basal cells point the relation of these remnants to *D. validus*. It is confirmed by the transverse section of costa with one row of guide cells, two well-developed stereid bands, and weakly differentiated ventral epidermis (Fig. 13D). Surface cells of costa are subquadrate to short-rectangular. However, the absence of whole leaves and scarcity of material make the species identity of these remnants unclear.

Didymodon sp. 2 (Fig. 14) is represented in the studied material by a single leaf 1.4×0.4 mm, with broken off uppermost tip (Fig. 14A). It is apparently keeled and reflexed, as it is seen from the side. It has an oblong base and comparatively short, triangular acumen. Its distal lamina cells are round, ca. 12 µm in diameter, thick-walled, smooth (Fig. 14B); basal juxtacostal cells are rectangular, 30–35×10–11 µm, thick-walled, basal marginal cells are shorter in 6 rows (Fig. 14C). This combination of characters suggests its placement into *D. asperifolius*, but it is impossible to be sure based on one leaf only.

Tortella splendida Köckinger & Hedenäs (Fig. 15). Two short fragments of shoots with linear-lanceolate, gradually tapered leaves apparently belong to the genus *Tortella*. One shoot, ca. 1 mm long, has most leaves with broken acumina (Fig. 15A); in another shoot 2.6 mm long, most leaves are entire, some of them S-shaped (Fig. 15D). Two partly broken leaves, 2.9×0.6 mm and 3.2×0.5 mm, are shown in Figs. 15B–C. Costa is strong, 120–150 µm at leaf base (Fig. 15G–H), short excurrent (Fig. 15J), in transverse section with one row of guide cells, two stereid bands and differentiated ventral and dorsal epidermices (Fig. 15F). Upper laminal cells quadrate, 8–10 µm wide (Fig. 15E), densely papillose (Fig. 15I), basal leaf cells rectangular, firm-walled, yellow, smooth, extending higher along margins, boundary between smooth and papillose cells U-shaped, gradual (Fig. 15H). The latter character allows us to identify this plant as *T. splendida* despite of one row of guide cells in transverse section of costa; in the Arctic plants, previously called *T. arctica*, two rows of guide cells are rarely observed (Ignatova *et al*., 2024).

Philonotis tomentella Molendo (Fig. 16). One fragment of shoot 13 mm long with pale, partly decomposed leaves (Fig. 16D) was found in the studied material. Almost entire leaf 0.6×0.2 mm with ovate base and triangular acumen is shown in Fig. 16B. It has percurrent costa, leaf margins plane, with small, paired teeth above, weakly recurved below; lamina cells rectangular, firm-walled, slightly narrower in the upper lamina (Fig. 16B), with single papilla at the lower end (Fig. 16A). This plant apparently belongs to *Philonotis tomentella* due to the cell shape and position of papillae, despite an unusually small size of leaves.

Meesia uliginosa Hedw. (Fig. 17). This species is represented by three fragments of leaves, 0.69–0.98 mm long and 0.14–0.17 mm wide (Fig. 17A–C); however, their species identity is straightforward due to strong costae



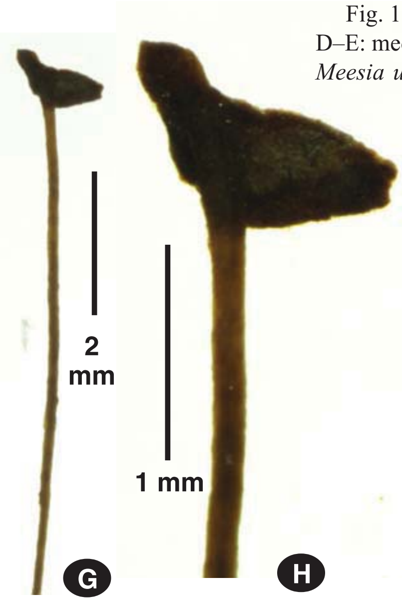
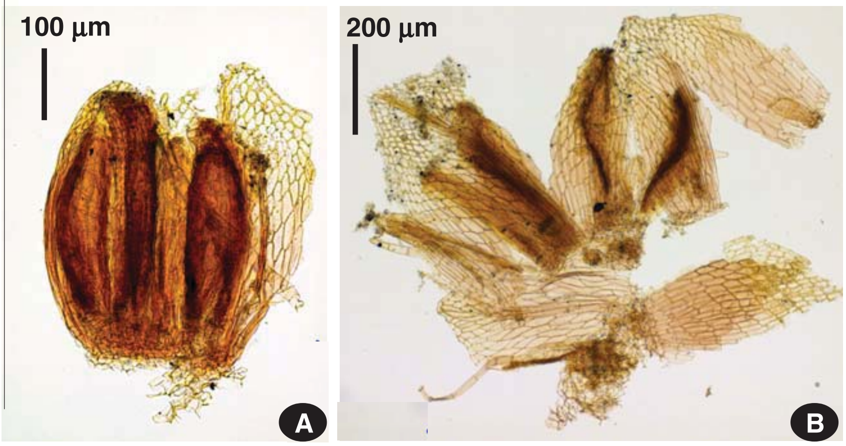
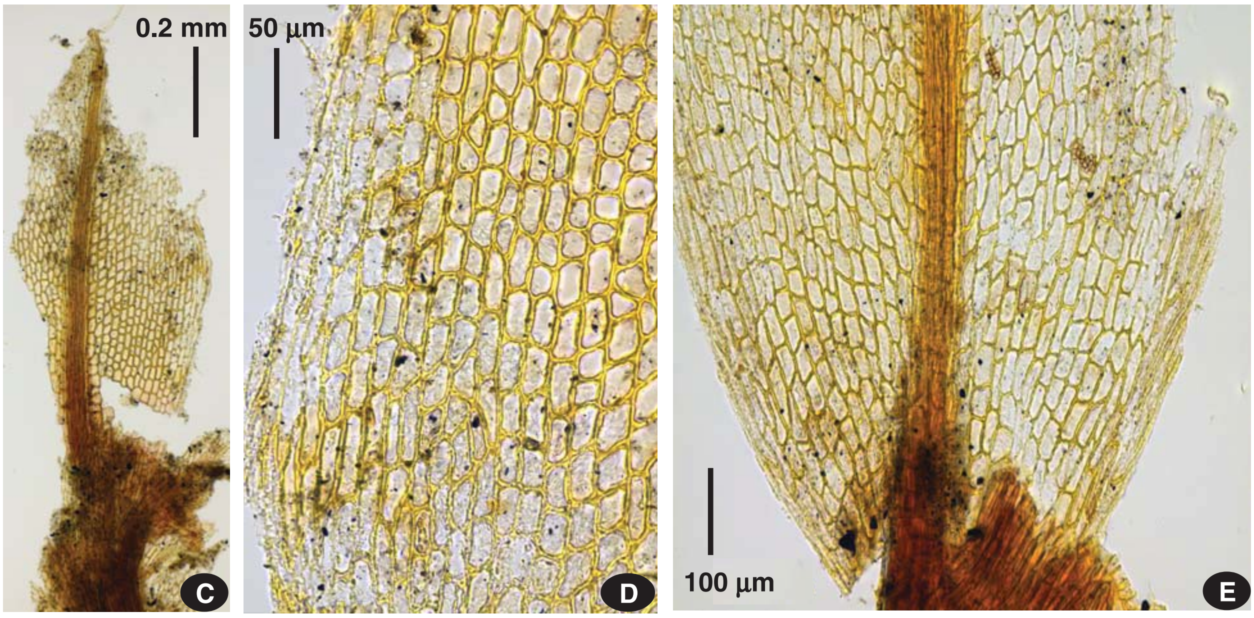


Fig. 17. *Meesia uliginosa* (#3_4A). A: leaf (#3_4A_1); B: leaf (#3_4A_2); C: leaf (#3_4A_3); D–E: median leaf cells (#3_4A_1); F: basal laminal cells (#3_4A_1); G–H: capsule, putatively of *Meesia uliginosa* s.l.

Fig. 18. *Bryum* cf. *cryophylum*. A–B: perigonia with old antheridia (#14_1_1; #14_1_2); C: leaf (#14_1_3); D: median leaf cells (#14_1_3); E: basal laminal cells (#14_1_4).





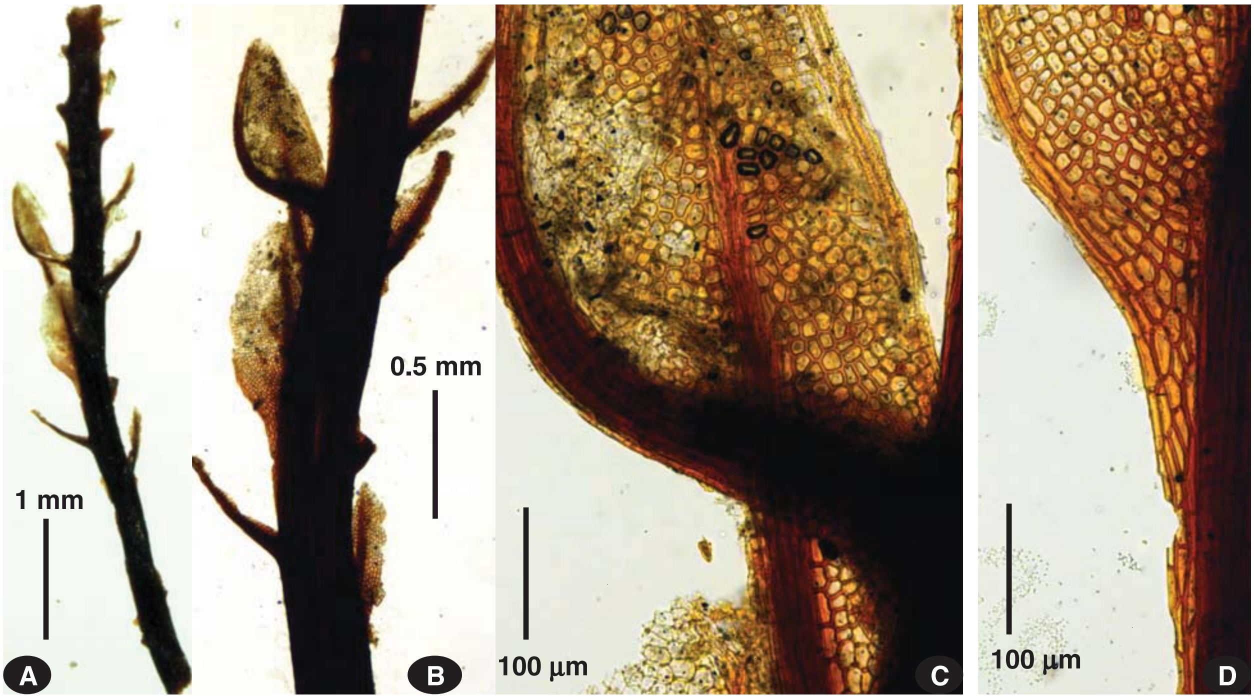


Fig. 19. *Cyrtomnium hymenophyllum* (#3_2_1 for all.). A–B: shoot; C: median leaf cells; D: cells of decurrency.

occupying half of leaf bases, 65–90 µm wide at base, gradually tapering upwards, and distinctly recurved leaf margins (Fig. 17D–E). There is also a capsule on long seta (Fig. 17G–H); its shape is not clearly seen because of distortion, but it possesses characteristic for *Meesia* curve at the transition from the neck to urn.

Bryum cf. ***cryophilum*** Mårtensson (Fig. 18). We refer to the genus *Bryum* one partly destroyed leaf 1.0×0.5 mm (Fig. 18C, D), one leaf fragment with well preserved basal part (Fig. 18E), two perigona, one with well preserved anteridia (Fig. 18A), and second with partly decomposed ones (Fig. 18B). Rhomboidal upper laminal cells and reddish-colored leaf base (Fig. 18E) make the generic placement of these remnants undoubted; however, it is more difficult to tell the species name due to the scarcity of material. We tentatively identify these plant remnants as *B. cryophilum* based on ovate leaf shape, subobtuse apex, weak marginal border, and dioicous sexual condition.

Cyrtomnium hymenophyllum (Bruch & Schimp.) Holmen (Fig. 19). One fragment of shoot 5.5 mm long, with two entire and several broken leaves apparently belongs to this species (Fig. 19A). It has distantly arranged, ovate leaves with costa ending below apex, isodiametric laminal cells 15–17 µm in diameter (Fig. 19B), marginal border formed by elongate cells (Fig. 19C), and long decurrencies (Fig. 19B, D).

Aulacomnium palustre (Hedw.) Schwägr. (Fig. 20). One shoot 1.9 mm long represents this species in the studied material (Fig. 20A). Its leaves are densely arranged, erect, ovate-lanceolate, with acute apices. Costa ends below leaf apex; laminal cells are isodiametric, collenchymatous, with single papilla over lumen.

Aulacomnium turgidum (Wahlenb.) Schwägr. (Fig. 21). Another species of *Aulacomnium* is represented by one shoot 4.8 mm long (Fig. 21A), with crowded, erect-spreading leaves, intact and with broken apices. Three almost entire leaves are shown in Fig. 21B–D. They are obovate, rounded, 2.7–2.8 mm long and 1.1–1.25 mm wide, with slender costae ending several cells below apices, margins revolute in proximal half (Fig. 21G). Laminal cells are isodiametric, 14–18 µm in diameter, strongly collenchymatous, with single papilla over lumen (Fig. 21E–F). This character combination makes the species identity of this remnant undoubted.

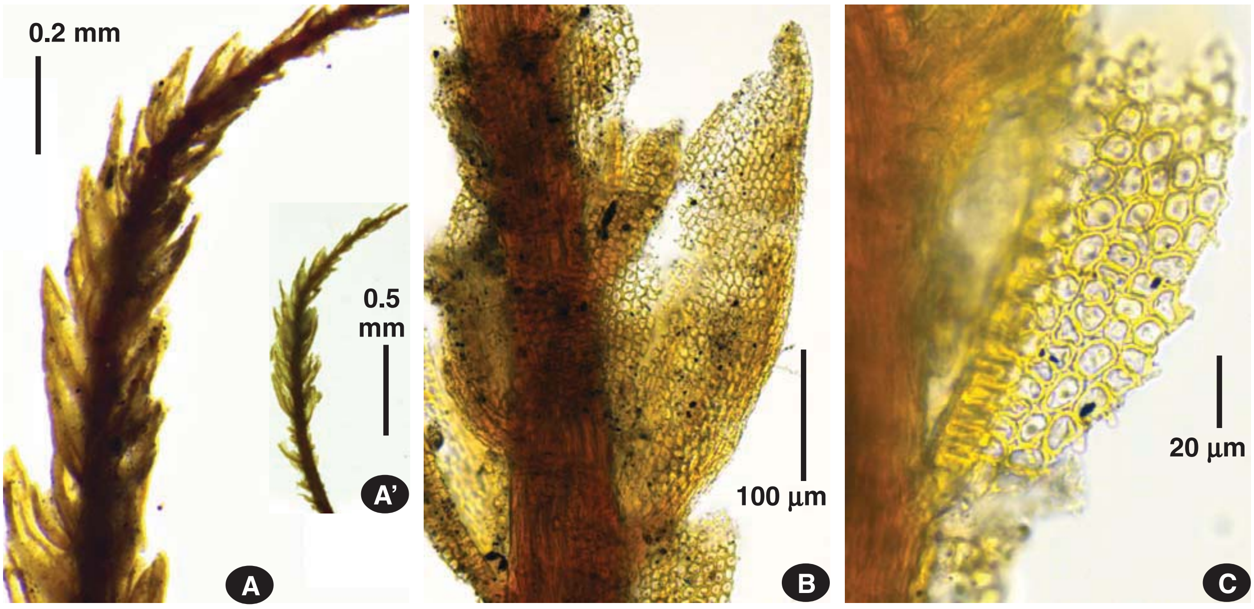


Fig. 20. *Aulacomnium palustre* (#8_1_1 for all). A–B: shoot; C: basal leaf cells.

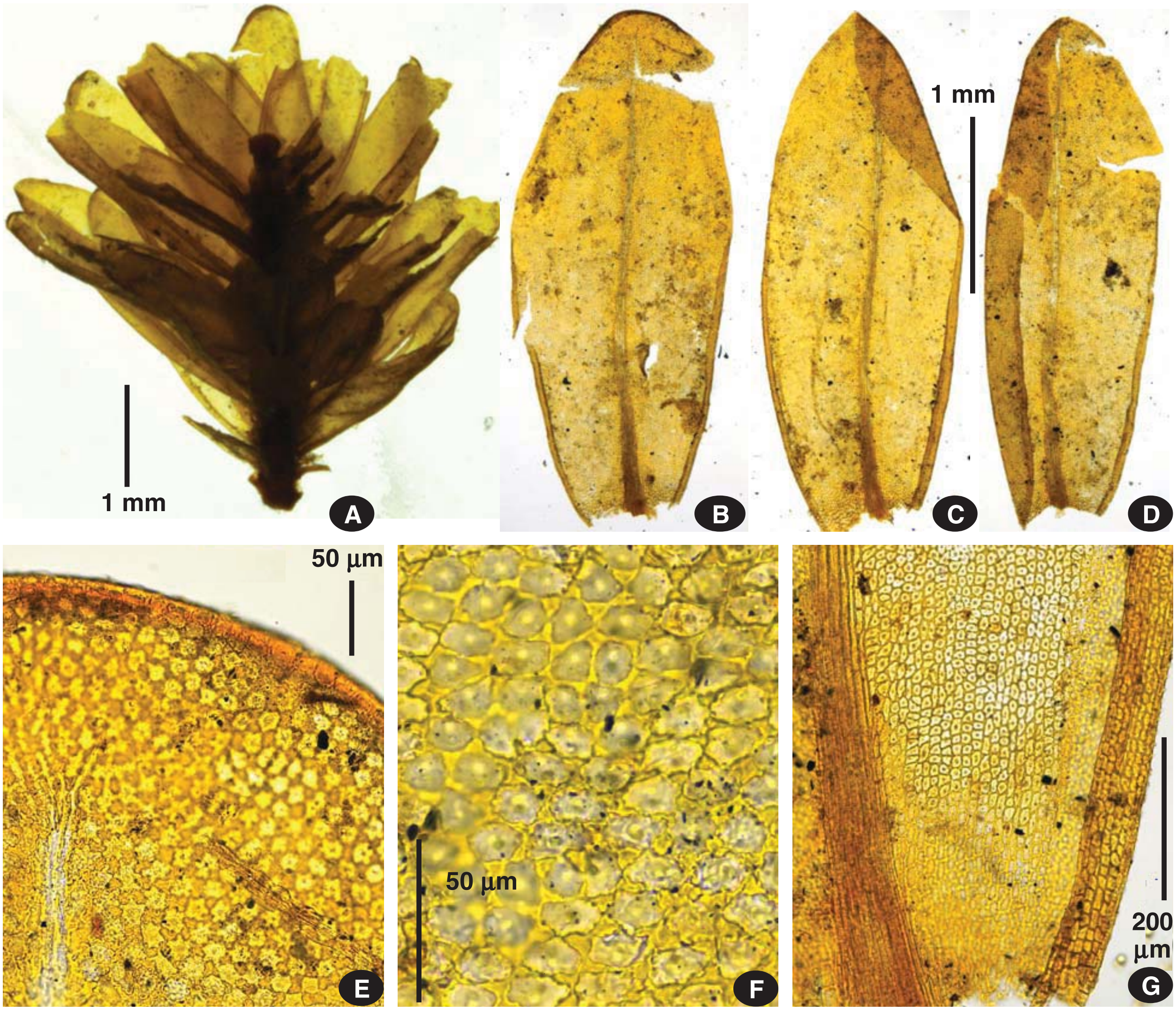


Fig. 21. *Aulacomnium turgidum* (#5_1A). A: shoot; B: leaf (#5_1A_1); C: leaf (#5_1A_2): D: leaf (#5_1A_3); E: upper lamina cells (#5_1A_1); F: median leaf cells (#5_1A_1); G: basal leaf cells (#5_1A_1).

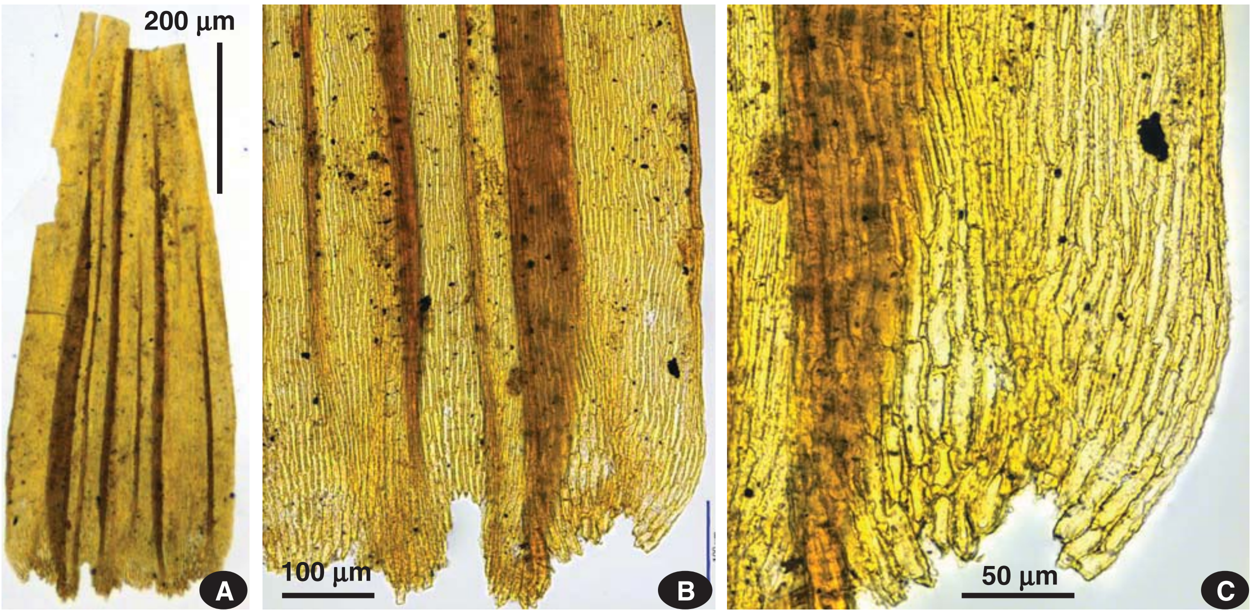


Fig. 22. *Orthothecium* cf. *chryseon* (#6_1A_2 for all). A: leaf; B: leaf base; C: alar cells.

Orthothecium cf. ***chryseon*** (Schwägr.) Schimp. (Fig. 22). Only one leaf, with broken off distal part, was found in the studied material (Fig. 22A). It is 0.7×0.3 mm, widest just above leaf insertion, gradually narrowing upwards, strongly plicate, with a short double costa hidden between plicae (Fig. 22B). Basal laminal cells are linear, 45–60×7–9 μm, thick-walled, porose. This combination of characters points most likely *O. chryseon*, despite the absence of apical part of leaf, so it is impossible to choose for sure between this species and *O. retroflexum*. This leaf fragment is also uncharacteristically small for both these species; however, so deeply plicate leaves are not known in other species of the genus with smaller leaves.

Isopterygiella pulchella (Hedw.) Ignatov & Ignatova (Fig. 23). We refer to this species one shoot ca. 3.4 mm long, with erect, slightly secund leaves (Fig. 23E).

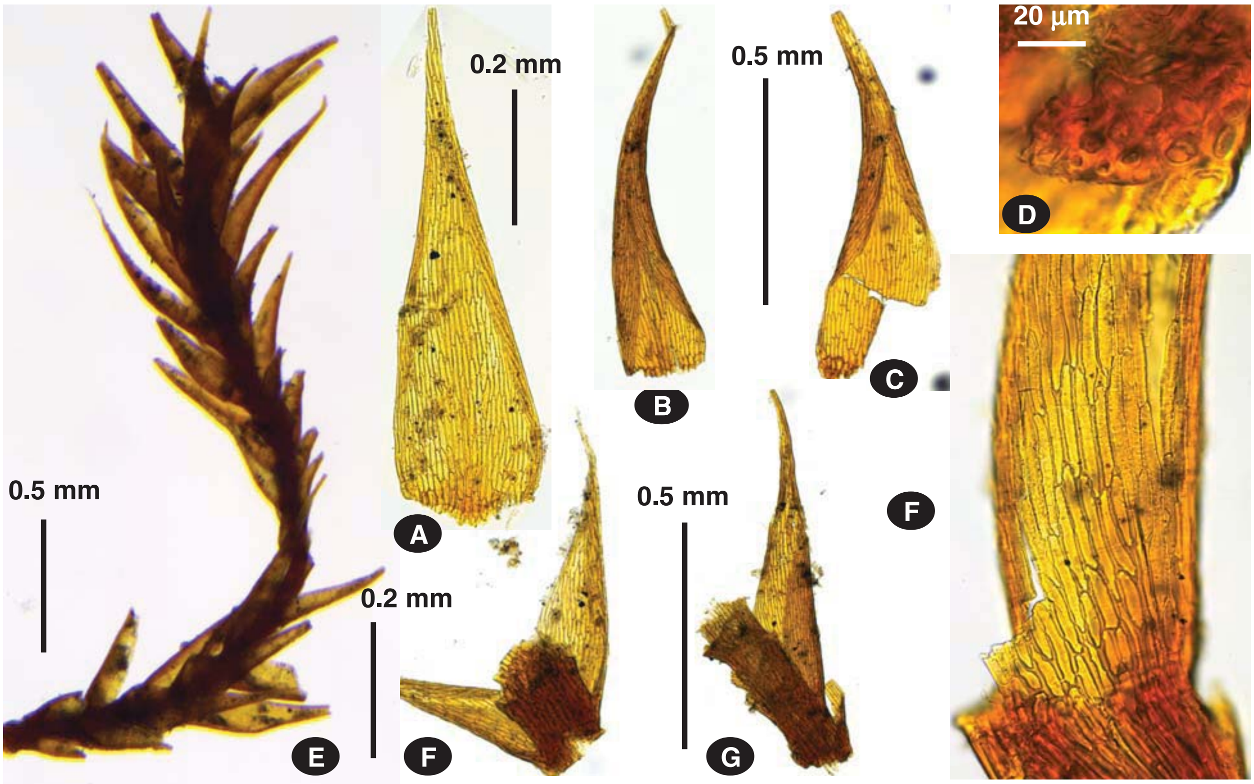


Fig. 23. *Isopterygiella pulchella*. A: leaf (#4_1B_1); B: leaf (#4_1B_2); C: leaf (#4_1B_3); D: alar cells (#4_1B_6); E: shoot; F: leaf with stem fragment (#4_1B_4); G: leaf with stem fragment (#4_1B_5); H: basal laminal cells ((#4_1B_5).

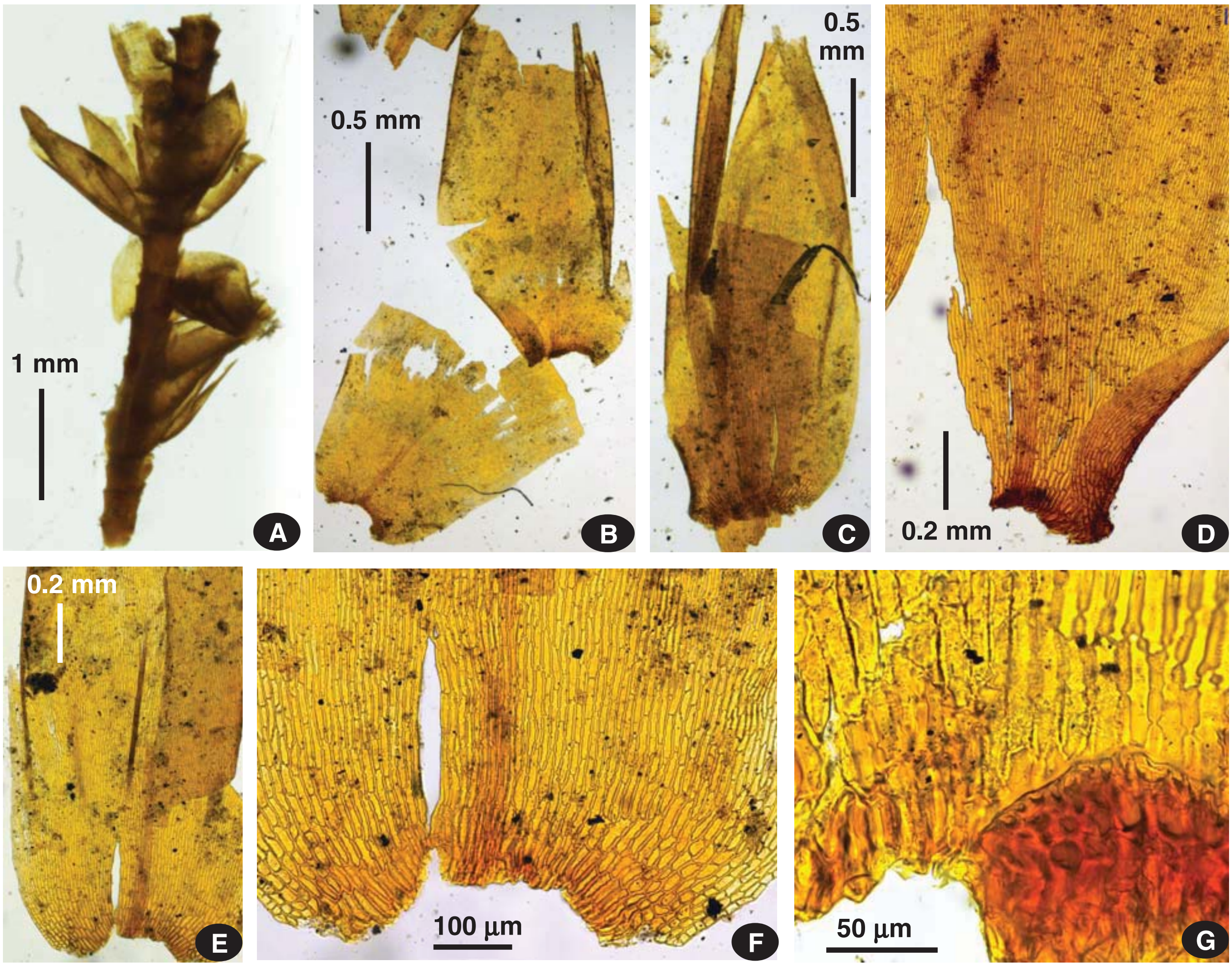


Fig. 24. *Pleurozium schreberi*. A: shoot; B: leaf (#2_1_2); C: leaf (#2_1_3); D: basal laminal cells (#2_1_4); E–F: basal laminal cells (#2_1_1); G: basal cells and a piece of stem sclerodermis (#2_1_2).

Leaves are lanceolate, 0.75×0.2 mm, widest slightly above insertion, gradually narrowing upwards, with entire margins, more or less concave, with short double costa (Fig. 23A–C, F–G). Laminal cells linear, 50–100×8–9 µm (Fig. 23A, F); alar cells not differentiated or few cells at insertion round, thick-walled, brown (Fig. 23F).

Pleurozium schreberi (Brid.) Mitt. (Fig. 24). This species is represented by one fragment of shoot 4.7 mm long with most leaves damaged (Fig. 24A). Two basal halves of leaves and one almost intact leaf 2.2×0.8 mm are shown in Figs. 24B–C. Leaves are ovate; all leaf apices are broken off, but they are apparently obtuse. Costa is short, double (Figs. 24B–F); leaf margins are entire (Fig. 24C); laminal cells linear, 50–75×9–11 µm, basal laminal cells porose, alar cells differentiated, subquadrate, thick-walled, porose, brown (Fig. 24F–G). A piece of sclerodermis attached to the leaf base (Fig. 24G) is red-brown, which confirms that this plant belongs to *Pleurozium schreberi*.

Hylocomium splendens (Hedw.) Bruch, Schimp. & W. Gümbel **subsp. *alaskanum*** (Lesq. & James) J.J. Amann (Fig. 25). Two short shoot fragments, 1.6 and 0.8 mm long, with several intact leaves definitely belong to this subspecies. Branched paraphyllia are clearly visible on branch stem (Fig. 25F) and at leaf base (Fig. 25D). Leaves are ovate, with obtuse apices (Fig. 25A–C); costa short, double (Fig. 25B, E); leaf margins entire (Fig. 24A); laminal cells 20–50×6–8 µm; alar cells not differentiated (Fig. 25A). One intact leaf 0.7×0.4 mm is shown in Fig. 25B; it is apparently a branch leaf from the primary branch.

Brachythecium tauriscorum Molendo & Lorentz (Fig. 26). The identity of one leaf fragment with broken off upper part is not certain (Fig. 26B). Its narrowly ovate shape and costa ending above mid-leaf, as well as alar groups extending along leaf margins suggest referring it to *Straminergon stramineum*. However, alar cells in the latter species are larger, thinner-walled, slightly inflated, which is not the case of the leaf in question. It is also possible to presume that its upper part was not rounded but acuminate. Combination of numerous, quadrate and rhomboidal, firm-walled alar cells, comparatively short median laminal cells, ca. 50 µm long, and narrowly recurved leaf margins fits well the circumscription of *Brachythecium tauriscorum*. This species is known from Chukotka, Vrangel Island, Verkhoyansky Mt. Range in

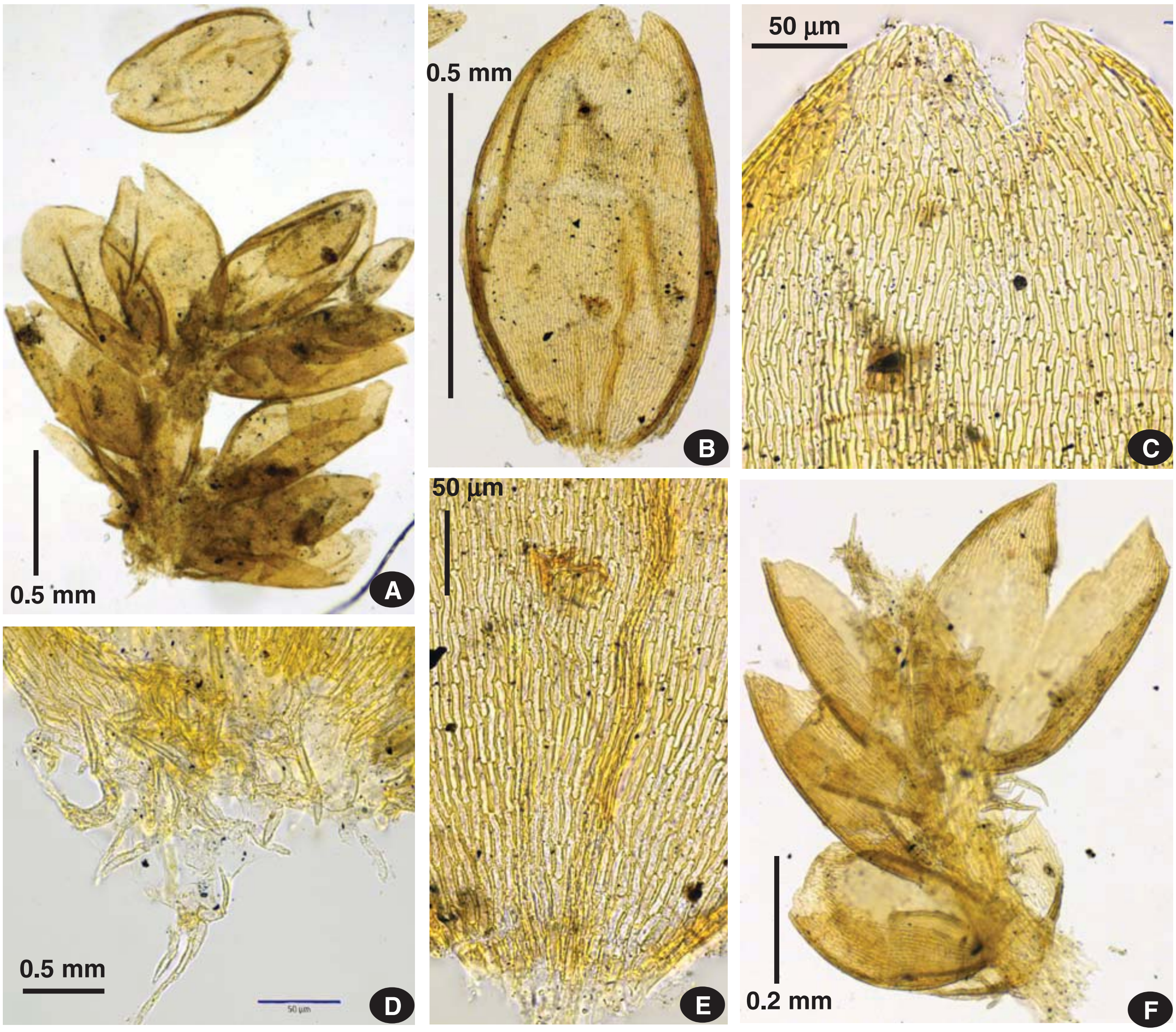


Fig. 25. *Hylocomium splendens* subsp. *alaskanum*. A: shoot; B: leaf (#16_2); C: upper laminal cells (#16_2); D: paraphyllia (#16_3); E: basal laminal cells (#16_2); F: shoot (#16_4).

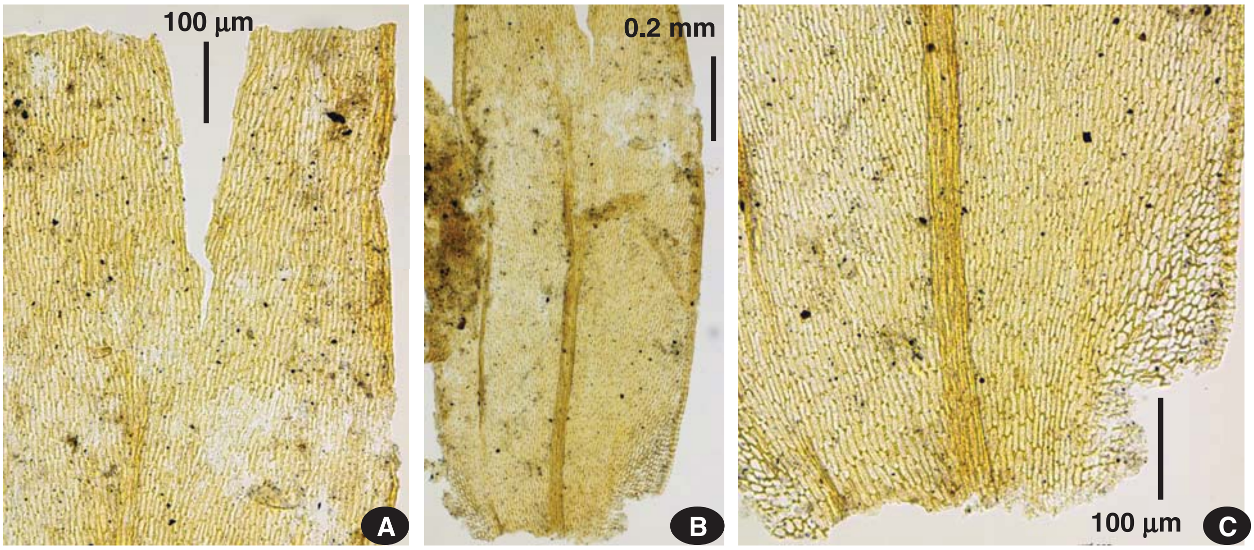


Fig. 26. *Brachythecium tauriscorum* (#4–2A_1 for all). A: mid-leaf cells; B: leaf; C: basal leaf cells.

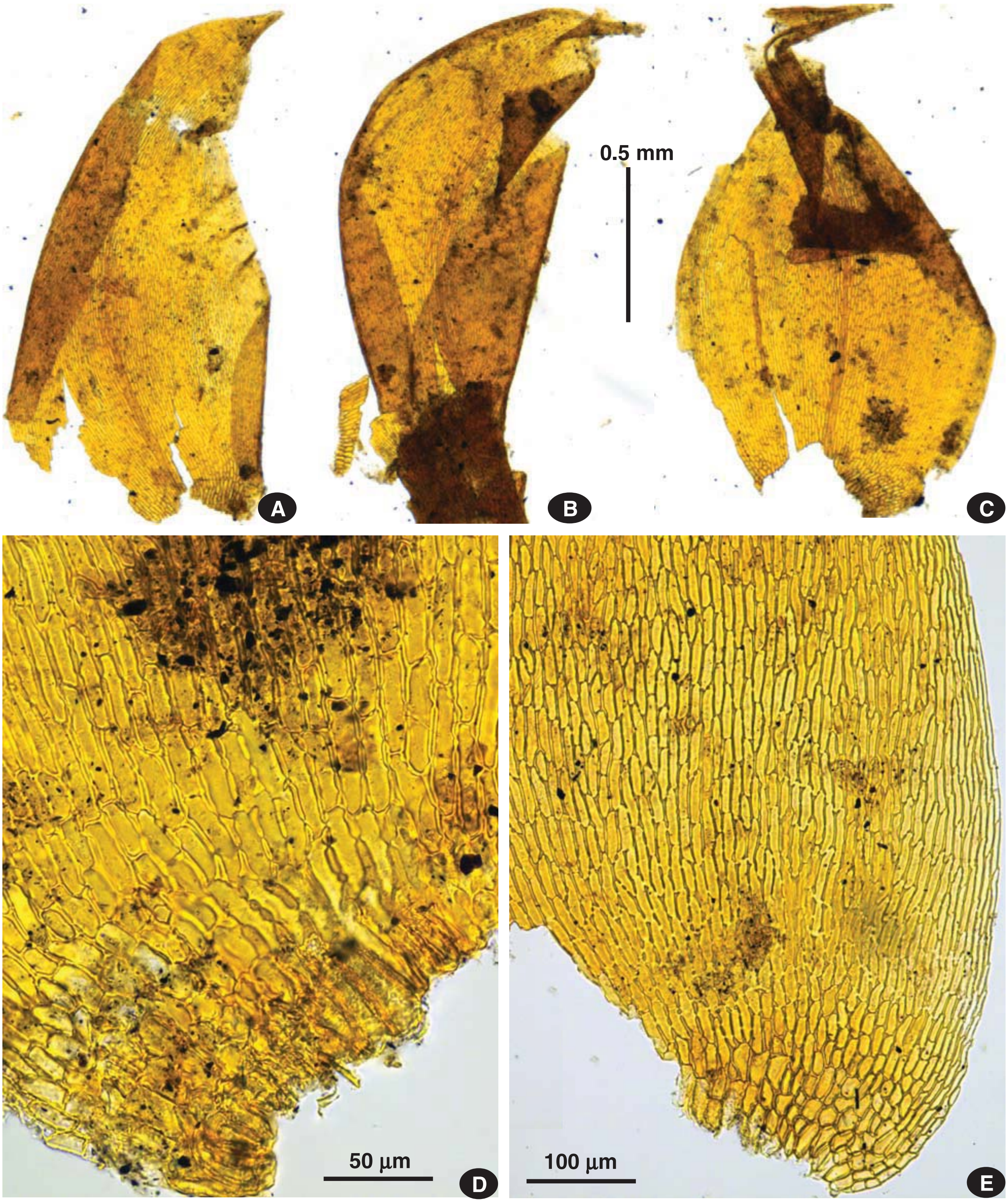


Fig. 27. *Loeskypnum badium*. A: leaf (#4_1A_1); B: leaf (#4_1A_2); C: leaf (#4_1A_3); D: basal laminal cells (#4_1A_3); E: alar cells (#4_1A_4).

Yakutia, and Taimyr, thus its presence in the Arctic Yakutia is quite possible.

Loeskypnum badium (Hartm.) H.K.G. Paul (Fig. 27). Three separate intact leaves 1.4–1.7×0.9–1.0 mm (Fig. 27 A–C) apparently belong to this species. They have ovate bases and short, attenuate acumina, weak single costa, subentire margins (Fig. 27E), thick-walled, porose laminal cells 45–60×10–12 µm (Fig. 27D–E), and small alar groups of short-rectangular cells with brownish walls (Fig. 27E).

Calliergon richardsonii (Mitt.) Kindb. ex G. Roth (Fig. 28). Two distal shoot fragments, 1.6 and 3.3 mm long (Fig. 28F–G) with appressed leaves were found in the studied material. Four leaves from these shoots are

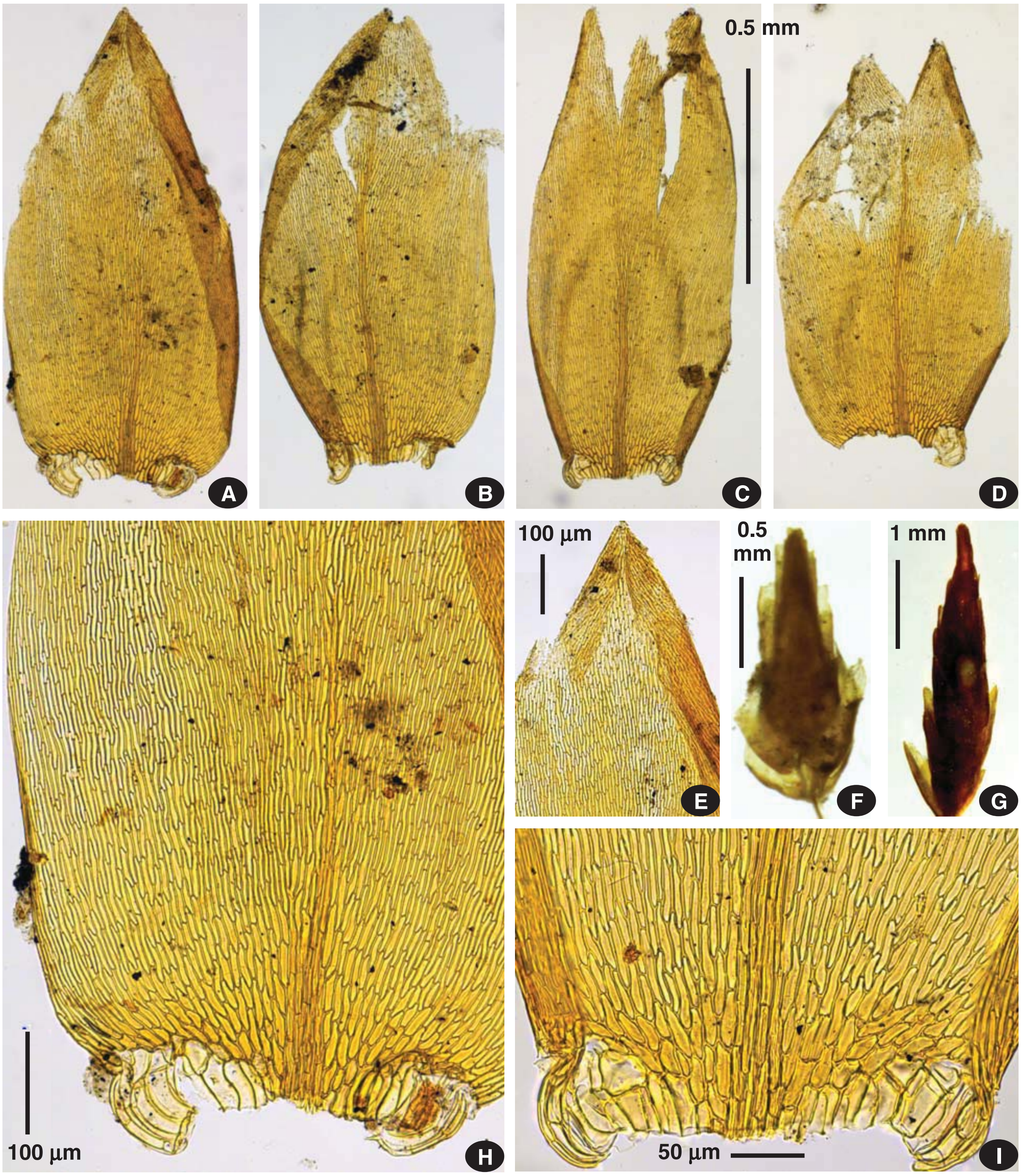


Fig. 28. *Calliergon richardsonii*. A: leaf (#5_2A_1); B: leaf (#5_2A_2); C: leaf (#5_2A_3); D: leaf (#5_2A_4); E: upper laminal cells (#5_2A_1); F, G: shoots; H: basal laminal cells (#5_2A_1); I: alar cells (#5_2A_3).

shown in Fig. 28A–D; two of them are intact and two have damaged apices. They are ovate, with rounded apices, 0.9–1.1×0.5–0.6 mm, with variable costae: double, with one branch to 1/3 of leaf length (Fig. 28A), forked, extending to mid-leaf (Fig. 28C), or single, ended at ca. 0.8 of leaf length (Fig. 28B, D). Alar groups are composed of inflated, hyaline cells; they are sharply delimited and extend to ca. 1/2 of the distance between margin and costa. This character combination makes identification of this plant unmistakable.

Scorpidium scorpioides (Hedw.) Limpr. (Fig. 29). At least two short shoot fragments of this species were found (Fig. 29A, I). Stem transverse sections revealed a hyaliodermis. Five leaves from these shoots are shown in Figs. 29D–H; they are ovate, concave, rounded and mostly ripped at apex, one leaf possessing a short apic-

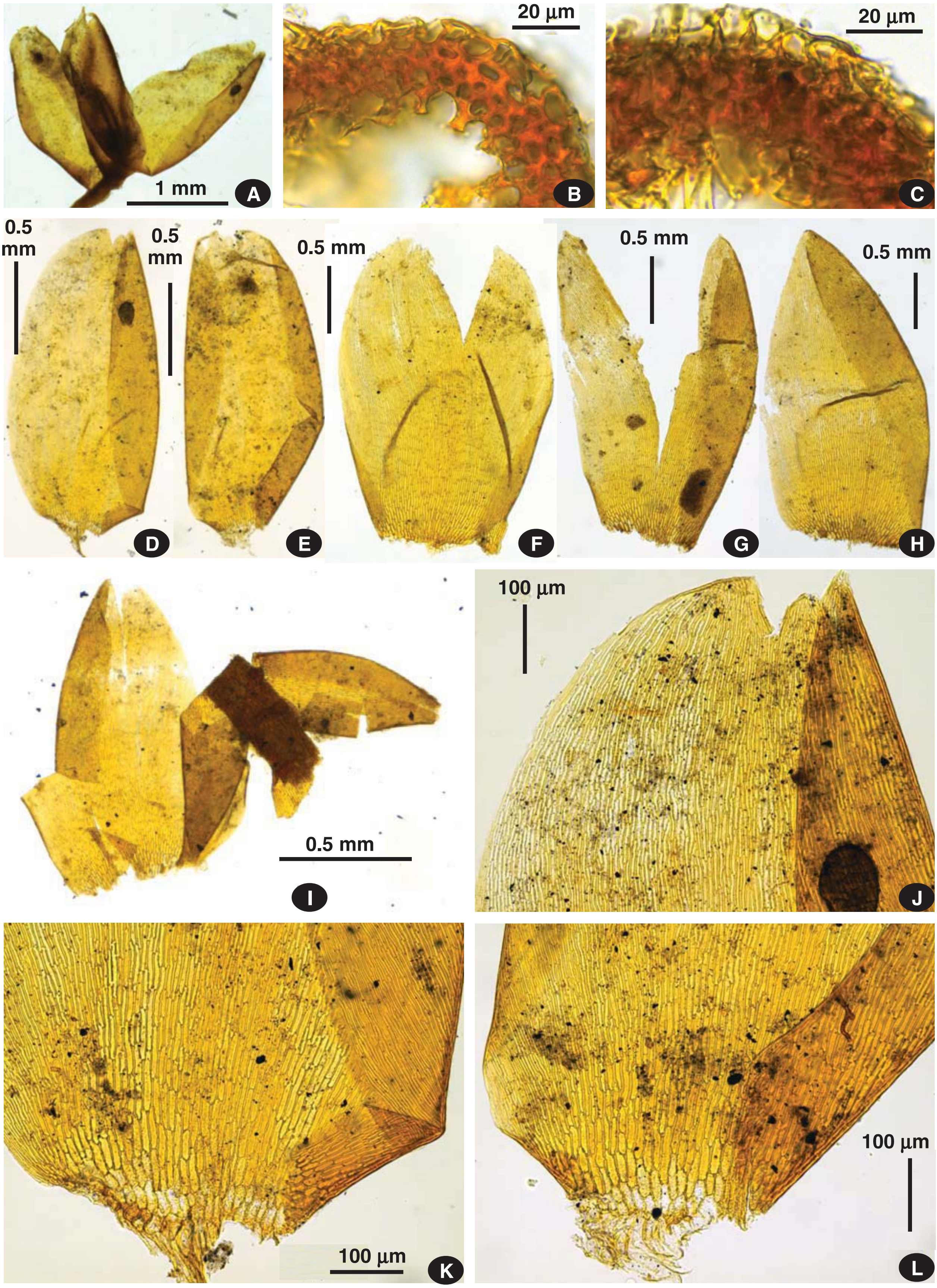


Fig. 29. *Scorpidium scorpioides*. A: shoot fragment; B: stem transverse section (#4_2B_1); C: stem transverse section (#4_2B_2); D: leaf (#4_2B_3); E: leaf (#4_2B_4); F: leaf (#4_2B_5); G: leaf (#4_2B_6); H: leaf (#4_2B_7); I: leaf and stem fragment (#4_2B_8); J: upper laminal cells (#4_2B_3); K: basal laminal cells (#4_2B_4); L: alar cells (#4_2B_3).

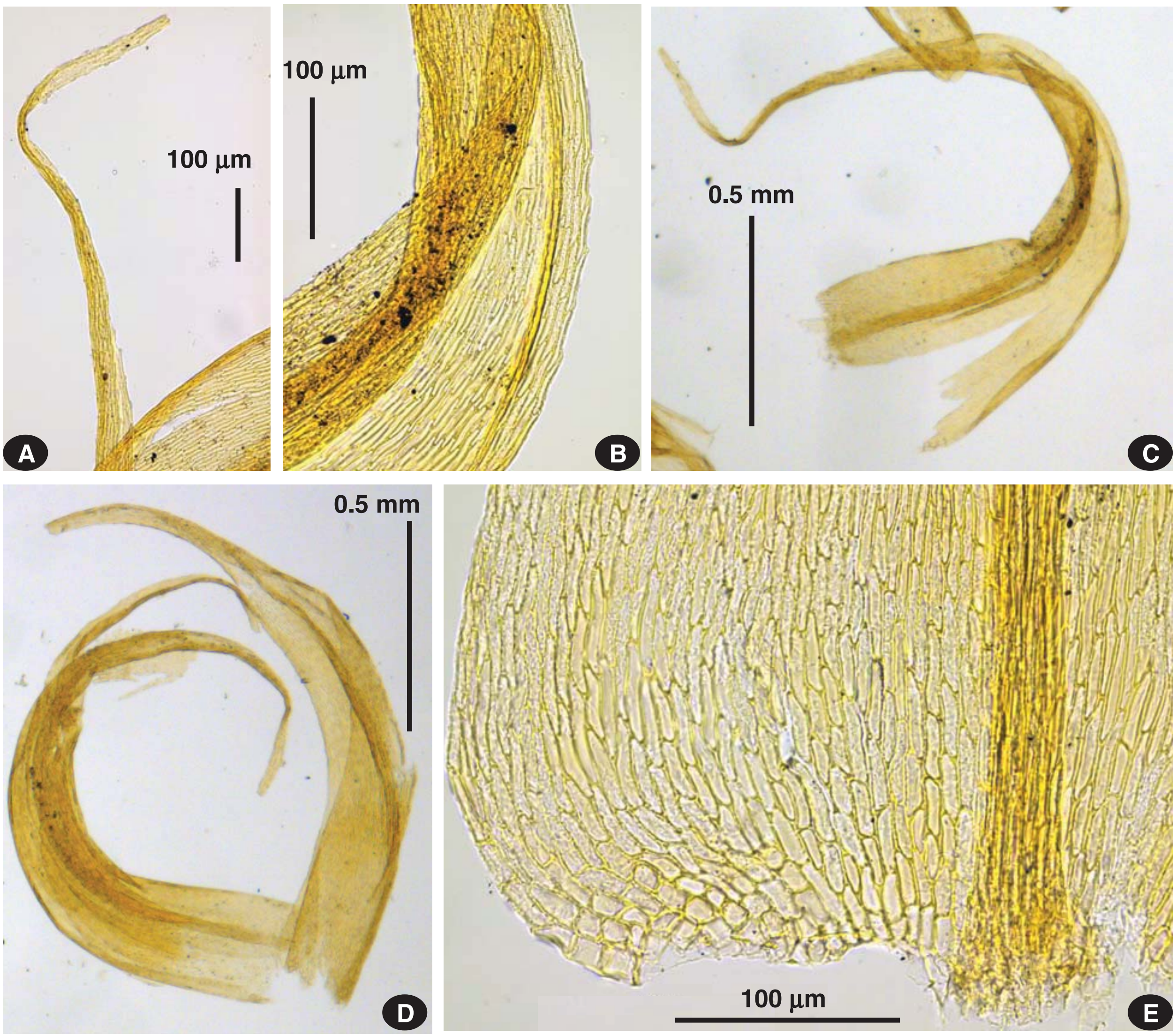


Fig. 30. *Sanionia uncinata*. A: upper laminal cells (#10_1); B: mid-leaf cells (#10_1); C: leaf (#10_1); D: leaf (#10_2&3); E: basal laminal cells (#10_4).

ulus (Fig. 29G). They vary in size from 1.6×0.9 mm to 2.7×1.6 mm; costa is very short and double; margins entire; laminal cells linear, 90–140 µm long (Fig. 29G); in one leaf (Fig. 29L) small alar group of hyaline, thin-walled, inflated cells is visible. We refer these remnants to *Scorpidium scorpioides* which is variable in leaf shape: almost orbicular, apiculate, or ovate-lanceolate, gradually tapering at apex (Hedenäs, 2008; Fuertes, 2018).

Sanionia uncinata (Hedw.) Loeske (Fig. 30). Three separate, almost intact leaves with only tips missing certainly belong to this species (Fig. 30C–D). They are 1.7×0.35 mm, 1.9×0.25 mm, and 2.2×0.4 mm, linear-lanceolate, narrowly acuminate, strongly falcate, with moderately strong single costae extending almost to the apex, indistinctly plicate, with serrate margins (Fig. 30A–B). Mid-leaf cells linear, 40–50 µm long; alar cells quadrate, forming a small alar group (Fig.30E). This combination of characters fits well *Sanionia uncinata*.

Leskea polycarpa Hedw. (Fig. 31). We refer to this species three separate leaves, one of them being almost intact and two damaged (Figs. 31 A–C). These leaves are widely ovate, 0.5–0.7×0.4–0.5 mm, acute, concave, with stout costa to 0.8 of the leaf length, margins entire (Fig. 31D). Laminal cells are rhomboidal, 10–16×7–8 µm, with one massive papilla over lumen (Figs. 31D, F–G); alar cells not differentiated (Fig. 31E).

Leskea polycarpa is widespread in Eurasia. In Asian Russia, it is more common in southern regions, but penetrates far to the north along valleys of major Siberian Rivers, including the Lena River, where it is common in middle course (Fig. 32). However, its localities closest to the place where the Bykovsky Mammoth was found are ca. 300 km to the south. *Leskea polycarpa* is primarily epiphytic species, growing in river valleys on willow trunks covered by alluvium. Its presence in the studied collection likely indicates warmer climatic conditions in Late Pleistocene, when this mammoth lived.

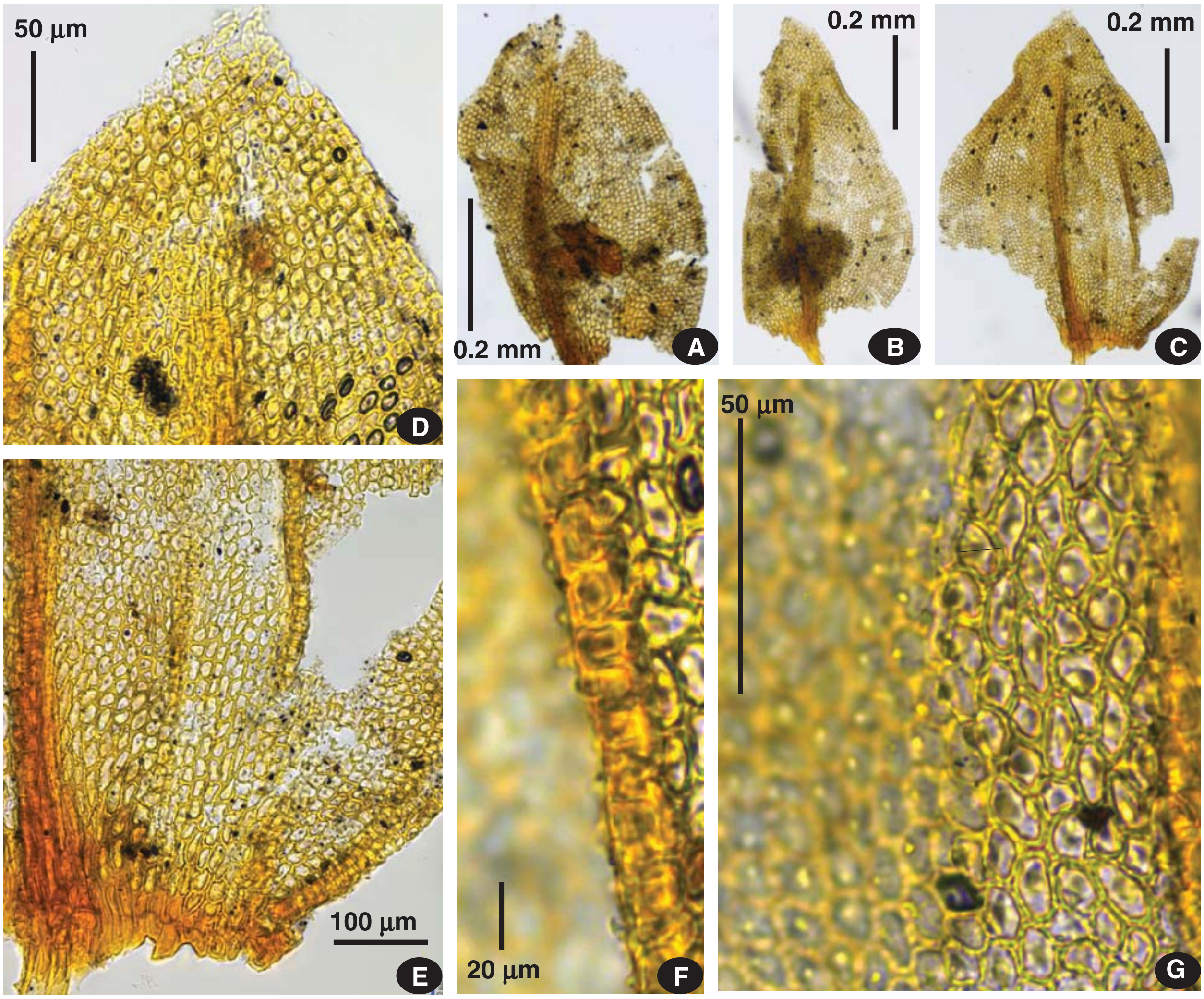


Fig. 31. Branch leaves of *Leskea polycarpa* (#3_1). A: leaf (#3_1_1); B: leaf (#3_1_2); C: leaf (#3_1_3); D: upper laminal cells (#3_1_3); E: basal laminal cells (#3_1_3); F–G: mid-leaf cells (#3_1_3).

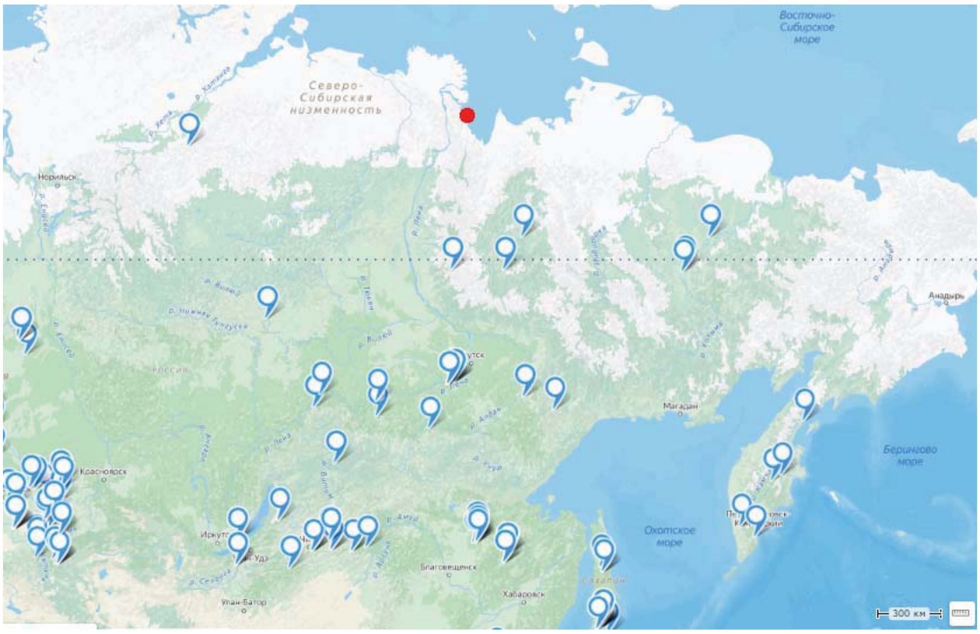


Fig. 32. Current distribution of *Leskea polycarpa* (based on the herbarium database of moss flora of Russia, http://arctoa.ru/en/Flora-en/basa.php) and its locality in the mammoth scull (red dot).

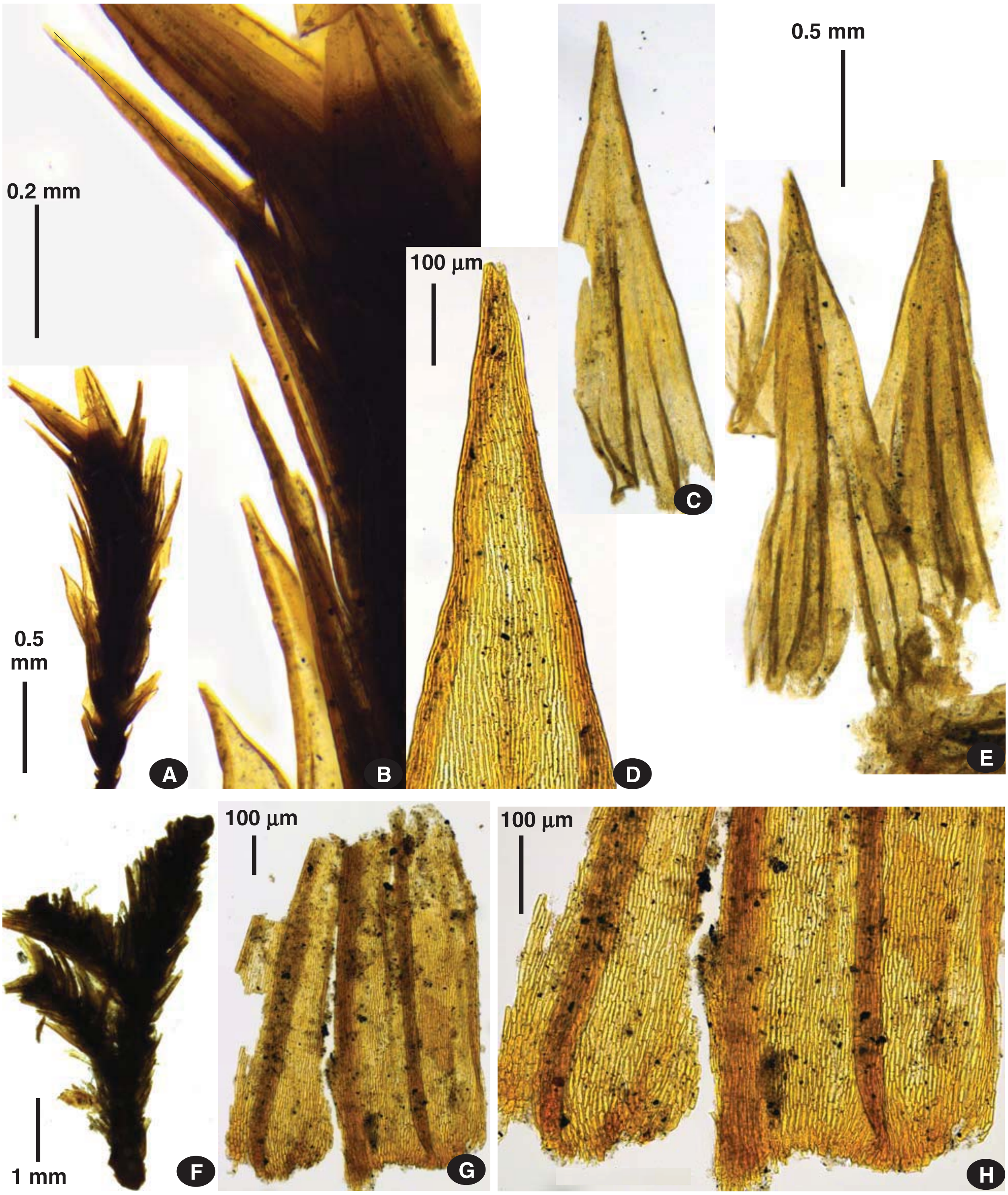


Fig. 33. *Tomentypnum involutum*. A–B, F: shoots; C: feaf (#16_5); D: upper laminal cells (#16_5); E: basal laminal cells (#16_6 & 7); G–H: mid-leaf and basal cells (#6_2B_1).

Tomentypnum involutum Hedenäs & Ignatov (Fig. 33). Two shoots with partly broken leaves, 2.3 and 5.9 mm long (Figs. 33A, F), apparently represent this species. One of these shoots has two branches. Leaves from these shoots are ovate-triangular, widest just above insertion, 1.7–1.9×0.6 mm, with single costa extending to 0.8–0.9 of leaf length, strongly plicate, laminal cells linear, 55–85 µm long, thick-walled, porose (Figs. 33C–H). Upper leaf margins are distinctly involute (Fig. 33D); this character makes species identification unequivocal. The poorly developed or even absent rhizoidal tomentum is another feature differentiating *T. involutum* from the more widespread *T. nitens,* although in severe climate of continental Yakutia the former species is locally more frequent.

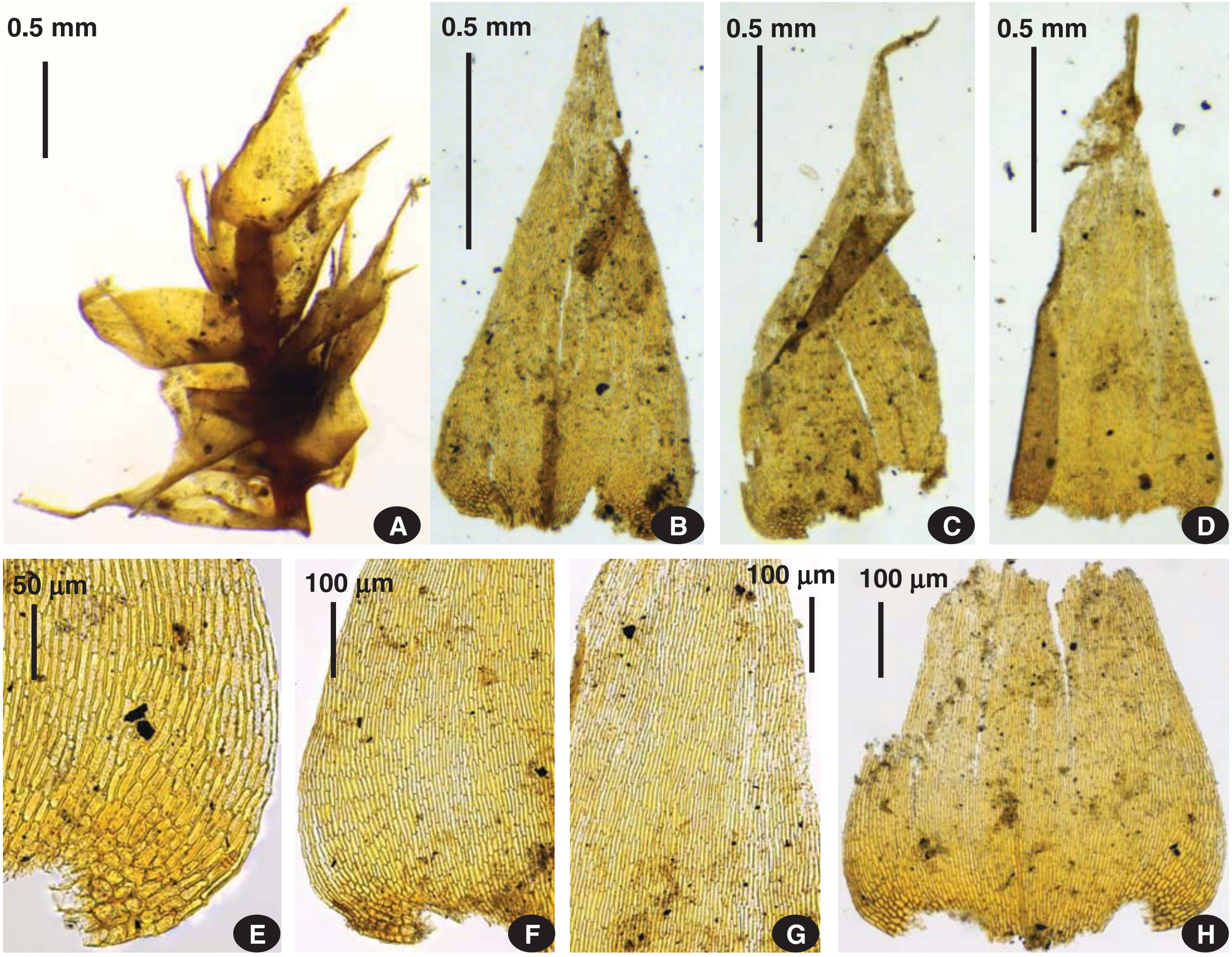


Fig. 34. *Campylium stellatum* (#3_3). A: shoot; B: leaf (#3_3_1); C: leaf (#3_3_2); D: leaf (#3_3_3); E: alar cells (#3_3_3); F: basal laminal cells (#3_3_4); G: mid-leaf cells (#3_3_3); H: leaf base (#3_3_5).

Campylium stellatum (Hedw.) Lange & C.E.O. Jensen (Fig. 34). One fragment of shoot 1.7 mm long, with almost intact, spreading leaves was found in the studied collection (Fig. 34A). Three leaves removed from this shoot are shown in Fig. 34B–D. They are ovate-triangular, 1.3–1.4×0.6–0.7 mm, gradually tapered upwards, narrowly acuminate, rounded to the insertion (Fig. 34E–F, H), not plicate, with short, double costae, and entire margins. Mid-leaf laminal cells are linear, 40–60×6–8 µm (Fig. 34G); alar cells differentiated, ovate, inflated, more or less thick-walled, forming small alar groups (Fig. 34E–F, H).

Hygroamblystegium varium (Hedw.) Mönk. (Fig. 35). We refer to this species a single shoot 5.7 mm long, with two branches, and with most leaves damaged (Fig. 34C). Leaf fragment, with upper third broken off, 0.3×0.16 mm, is shown in Fig. 34B. Leaf shape is apparently lanceolate, margins serrulate; costa single, long, laminal cells 2–3:1, 15–25×6–7 µm; alar cells weakly differentiated, few, quadrate and short rectangular. A branch primordium can also be observed on this shoot (Fig. 34A); its structure fits well the family Amblystegiaceae, as the proximal branch leaves keep the lateral position, as in most pleurocarpius mosses. This feature is shown here for this specimen since the short lamina cells and long costa are the combination indicating *Sciuro-hypnum reflexum*. The Brachytheciaceae, however, have the first proximal branch leaf pointing downward, that would be easily seen in such case. This combination of characters suggests identifying this remnant as *Hygroamblystegium varium* due to costa geniculate distally (Fig. 34B) despite the broken off leaf apices does not allow us to see clearly the costa ends.

Drepanocladus trifarius (F. Weber & D. Mohr) Broth. (Fig. 36). Two shoot fragments, 4.1 and 4.3 mm long (Figs. 36A–B) are referred to this species. The first one, apparently representing distal part of stem, has most leaves almost intact. One of these leaves is shown in Fig. 36C–E); it is almost orbicular, 1.3×1.0 mm, with round apex and very thin costa ceasing below apex; laminal cells are linear, ca. 35–50 µm long, moderately thick-walled, aporose or slightly porose (Fig. 36D); basal cells wider, thicker-walled, porose, alar cells not differentiated (Fig. 36E). This combination of characters fits well *D. trifarius*.

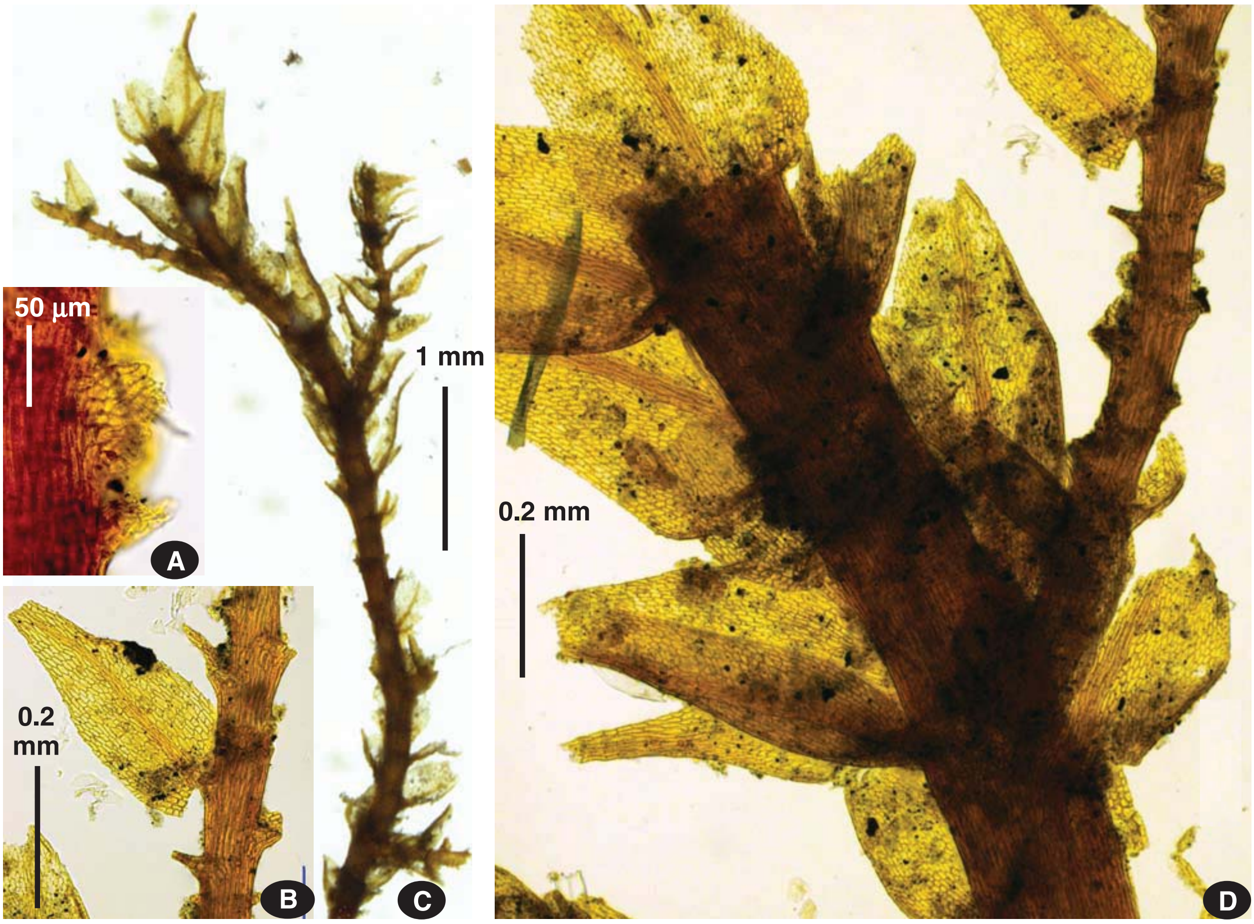


Fig. 35. *Hygroamblystegium varium* (#6_1B_1 for all). A: branch primordium; B: leaf; C–D: shoots.

Drepanocladus brevifolius (Fig. 37). Remnants of this species are especially abundant in the studied material. One fragment of an apical portion of shoot, 4.6 mm long (Fig. 37A) and another from the shoot middle, 2.8 mm long (Fig. 37B) have most leaves intact. Stems lack hyalodermis (Fig. 37I). Branch primordia are conspicuous, with wide, rounded leaves (Fig. 37F). Leaves are strongly falcate-secund, 1.5–1.6×0.5–0.6 mm (Fig. 37D, G–H), with ovate bases, rounded to the insertion, with short acumina; costa is thin, occasionally forking or 'diluting' (Fig. 37H, K), margins are widely incurved distally, entire (Fig. 37C, J). Laminal cells are comparatively short, 30–50(–60)×7–8 µm, moderately thick-walled (Fig. 37K); basal cells are shorter, thicker-walled, porose (Fig. 37M), alar cells small, isodiametric, thick-walled, forming small alar groups (Fig. 37L). Distal laminal cells look smooth or almost so in transmitted light (Fig. 37C), while having a somewhat prorate aspect in darkfield condenser view (Fig. 37E). Prorate cells disagree with *D. brevifolium*, but occur occasionally in a closely related *D. angustifolium* (Hedenäs) Hedenäs & S. Rasborg. However, the latter species differ from our specimens in long acuminate leaves with serrulate margins, and strong, invariably single costa (Hedenäs & Miller, 2014).

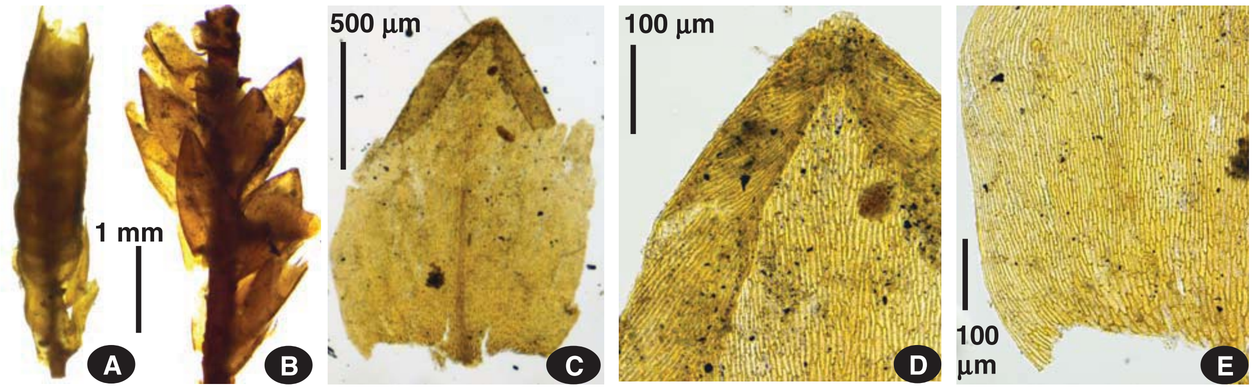


Fig. 36. *Drepanocladus trifarius*. A: shoot tip; B: shoot middle part; C–E (#3_3_6): C: leaf; D: distal leaf portion; E: leaf base.

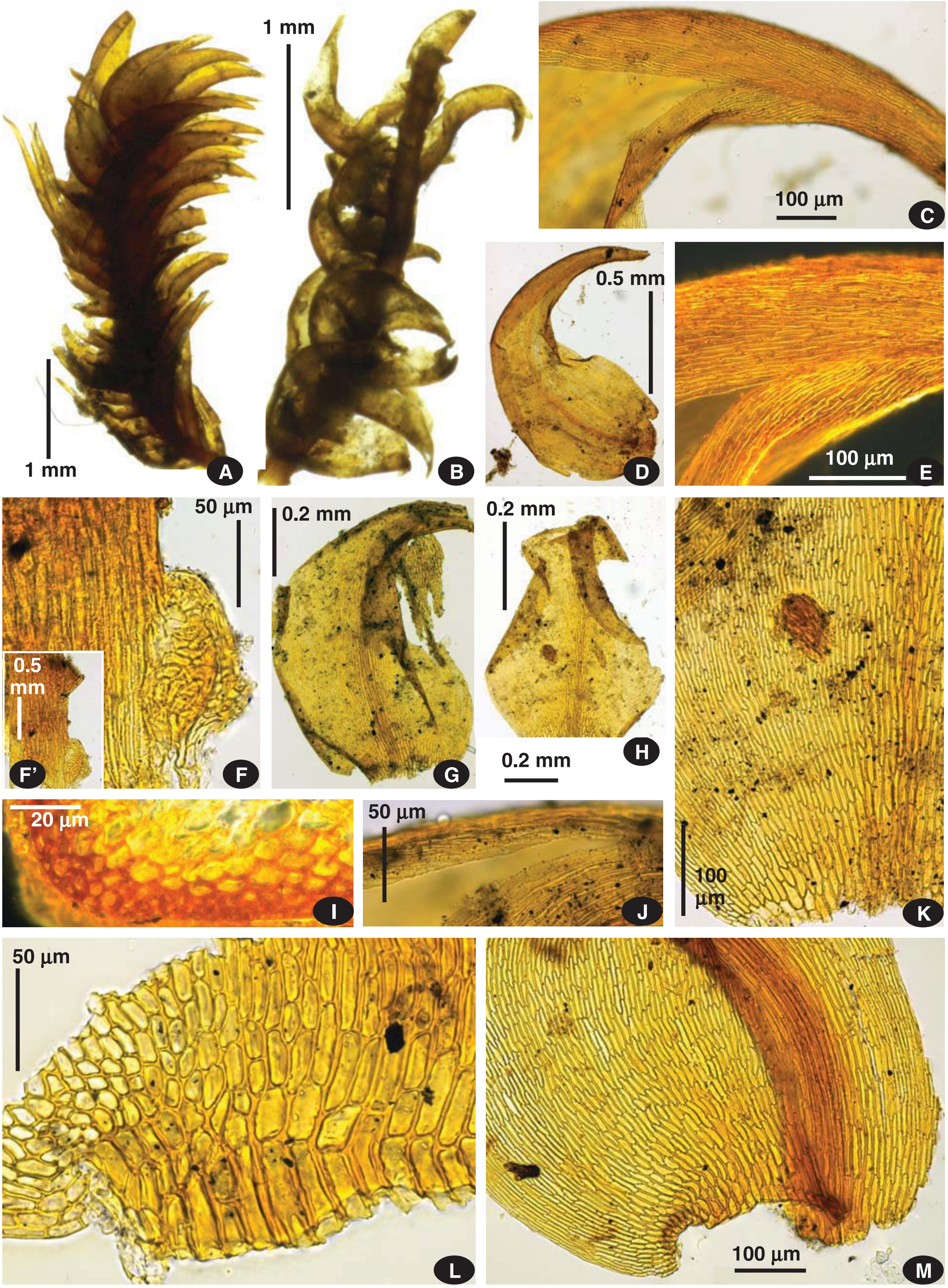


Fig. 37. *Drepanocladus brevifolius*. A, B: shoots; C, E: leaf acumen (#6_0_1); D: leaf, darkfield condenser image (#6_0_1); F: branch primordium (#6_2); G: leaf (#6_2B_3); H: leaf (#6_2B_2); I: stem transverse section, darkfield condenser image (#19_3); J: distal leaf cells (#6_2B_3); K: basal leaf cells (#6_2B_2); L: basal laminal cells (#19_2); M: basal laminal cells (#19_1).

Table 1. Late Pleistocene mosses in the gastrointestinal tracts of fossil mammals inYakutia in five localities (with age and reference): 1 – Berezovsky Mammoth (44000±3500 yr, Ukraintseva, 2002); 2 – Shandrinsky Mammoth (40350±880 yr, Ukraintseva, 2002); 3 – Selerikanskaya Horse (38590 ± 1120 yr, Ukraintseva, 2002); 4 – Mylachikhionsky Bison (29500±1000, Ukraintseva, 2002); 5 – Yukagirsky Mammoth (18510±100 лет, Van Geel *et al*., 2008). «X» plant macrofossils, «+» spores.

Species	1	2	3	4	5
Abietinella abietina			X		
Aulacomnium turgidum	X	X			
Bryum sp. 1			X		
Bryum sp. 2				X	
Calliergon sp.			X		
Distichium capillaceum			X		
Dicranum sp.		+			
Drepanocladus aduncus					X
Drepanocladus fluitans	X				
Drepanocladus sp.			X		
Entodon concinnus					X
Polytrichum commune		X			
Polytrichum strictum		X	X		
Polytrichum sp. 1		+	X		
Polytrichum sp. 2			X		
Polytrichum sp. 3				X	
Pottia sp.				+	
Rhytidium rugosum			X		
Sphagnum angustifolium		X			
Sphagnum girgensohnii		X			
Sphagnum sp. 1		X+	X		
Sphagnum sp. 2			X+		
Sphagnum sp. 3				X+	
Sphagnum sp. 4					X
Sphagnum sp. (sect. *Palustria*)		X			
Sphagnum sp. (sect. *Subsecunda*)		X			
Syntrichia ruralis			X		
Thuidium sp.			X		
Tomentypnum nitens		X		X	
Bryales	+	+	+	X+	

DISCUSSION

Advantage of the bulk maceration

This method is comparatively laborious and can be considered as a superfluous for providing merely a list of species; however, the present example demonstrates its usefulness. Standard washing of the material used in previous studies most commonly allowed identification only to the genus level (Table 1), whereas in our study bulk maceration resulted in obtaining cleaner material, comprehensive for identificaltion 32 out of 35 mosses to the species, and less than 10% to the genus level.

The obtained material was sufficient for identification of difficult and only slightly differentiated species, e.g., *Tomentypnum involutum*. Until recently, it was considered merely as a variety of the widespread Holarctic species *Tomentypnum nitens*. Taxa at such rank are usually neglected in biodiversity studies, thus it remained little known. *Tomentypnum involutum* was recognized as a distinct species in the molecular phylogenetic study (Hedenäs *et al*., 2020) and appeared to be quite revealing geographically, being confined to the area with the Pleistocene-like tundra-steppe biota. The largely intact leaves obtained from the bulk maceration probes were sufficient to confirm it in the Bykovsky Mammoth. Another example is *Hygroamblystegium varium*; the remnant was originally assumed as a depauperate *Sciuro-hypnum reflexum*, but this decision was rejected later, when proximal branch leaves around branch primordia were studied. This character requires clear vision of stem surface in between leaves (Ignatov, 1999), which appeared to be possible for the sample in question. Also, a possibility to cut stem and leaves was very helpful. We were able to confirm the presence of hyalodermis, which is important for identification of pleurocarpous mosses. Likewise, investigation of costa anatomy, especially for stereid bands, was crucial for identification of species from the difficult family Pottiaceae, including *Didymodon* and *Tortella* in our collection. The Polytrichaceae species, especially those closely related to *Polytrichastrum alpinum,* also require sections of costa for identification, as they are distinguished by shape and papillosity of the apical cell of the coastal lamellae.

Certainly, more possibilities may appear if the bulk maceration method will be applied to well preserved but buried in frozen soil plant material (cf. Fig. 2A). Of course, the quantity and preservation of mosses are also very important.

A comparison with Kirgilyakh Mammoth

The outstanding moss diveristy associated with mammoth was found in Kirgilyakh Mammoth (Abramov & Abramova, 1981), which age has been identified as 41000±900 yr (Shilo & Lozhkin, 1981). Mosses were abundant in soil around the mammoth baby's body and provided a comprehensive collection of 44 species, identifdied mostly to the species level, with only 9 specimens referred to the genus (Table 2).

In addition, Nikitin (1981) analised the gastrointestinal tract of that mammoth baby. He reported from the colon *Pleurozium* sp., *Calliergon* sp.?, and Bryales indet., and from the rectum *Aulacomnium sp., Helodium sp., Calliergon* sp., and '*Mnium affine*'; the latter species was understood that time more broadly, it included *Plagiomnium ellipticum*, to which it apparently belongs.

Ukraintseva (1981) additionally reported *Sphagnum angustifolium*. According to her, different parts of the mammoth body and soil around it contained spores of *Sphagnum* (2.8–21.6% of pollen & spore spectra) and 25.0–32.4% of other mosses.

Environment of Kirgilyakh Mammoth was evaluated as swampy tundra or dry tundra, with *Pinus pumila*, and probably with *Larix*. The pollen of the latter tree was solitary, but even then its presence makes the presence of open *Larix* stands quite likely, considering that its pollen is hardly preserved (Ukraintseva, 1981).

Table 2. Comparison of mosses from the locality of Kirgilyakh Mammoth (Abramov & Abramova, 1981), with 3 additional species, marked with * from Nikitin (1981) and Ukraintseva (1981), mentioned in the text, and Bykovsky Mammoth (see Results). Underlined are species in common for both localities

Kirgilyakh Mammoth	Bykovsky Mammoth
*Sphagnum angustifolium**	*Sphagnum sp.*
Sphagnum russowii	
Sphagnum teres	
Pogonatum urnigerum	
Polytrichastrum alpinum	*Polytrichastrum alpinum*
	Polytrichastrum septentrionale
Polytrichum strictum	*Polytrichum strictum*
	Polytrichum juniperinum
Encalypta sp.	*Encalypta alpina*
	Encalypta procera
Niphotrichum canescens	
Flexitrichum flexicaule	*Flexitrichum flexicaule*
Distichium capillaceum	*Distichium capillaceum*
	Fissidens adianthoides
Dicranella sp.	
Dicranum flexicaule	
Ceratodon purpureus	
Trichostomum sp.	
Tortella sp.	*Tortella spendens*
Tortella fragilis	
Syntrichia ruralis	
Pottia sp. (Tortula p.p.)	
Tortula mucronifolia	
	Didymodon borealis
	Didymodon sp. 1
	Didymodon sp. 2
	Meesia uliginosa
Philonotis sp.	*Philonotis tomentella*
Bryum sp	*Bryum cryophilum*
Pohlia sp.	
Pohlia cruda	
Mnium lycopodioides	
Mnium spinosum	
Plagiomnium ellipticum	
	Cyrtomnium hymenophyllum
Aulacomnium palustre	*Aulacomnium palustre*
Aulacomnium turgidum	*Aulacomnium turgidum*
	Orthothecum cf. *chryseum*
	Isopterygiella pulchella
Myurella tenerrima	
Hypnum cupressiforme	
*Pleurozium sp.**	*Pleurozium schreberi*
	Hylocomium splendens
Eurhynchiastrum pulchellum	
	Brachythecium tauriscorum
Brachythecium sp.	
Brachythecium cirrosum	
Calliergon giganteum	
	Calliergon richardsonii
	Loeskypnum badium
Straminergon stramineum	
Warnstorfia fluitans	
	Scorpidium scorpioides
	Sanionia uncinata
Entodon concinnus	
Rhytidium rugosum	
Pseudoleskeella tectorum	
	Leskea polycarpa
Abietinella abietina	
Thuidium assimile	
*Helodium sp.**	
	Tomentypnum involutum
Tomentypnum nitens	
Campylium protensum	*Campylium stellatum* s.l.
Campylium chrysophyllum	
	Hygroamblystegium varium
	Drepanocladus brevifolius
	Drepanocladus trifarius
Drepanocladus aduncus	

The list of mosses (Table 2) for Kirgilyakh Mammoth includes some mire species (*Sphagnum teres, Straminergon stramineum, Warnstorfia fluitans*), while most species are mesic, now occurring in Yakutia in open forests, on various eroded slopes, in tundra-like vegetation scattered among *Larix* forests. The revealing for the general assessment of situation is the absence of *Hylocomium splendens* and probably also of *Pleurozium schreberi* (a specimen indefinitely named and poorly preserved in the colon may not be a reliable evidence). At the same time, the presence of the *Rhytidium rugosum, Abietinella abietina,* and *Entodon concinnus* is noteworthy. These three species not found in Bykovsky Mammonth dominate now in more xeric variants of tundra and in open *Larix* forests in Yakitia, mountains of south part of Siberia, and in Mongolia. Recent biodiversity studies in East Yakutia at latitude 60–65°N show that almost all moss species from the Kirgilyakh Mammoth locality occur in every studied area (Ignatov *et al.*, 2001; Ignatova *et al.* 2011, 2018, 2020; Isakova, 2010; Ivanova *et al.*, 2016, 2017, 2018). Abramov & Abramova (1981) also concluded that the species composition indicate dry mountain tundra.

The mosses of Bykovsky Mammoth indicate a very different environments from that of Kirgilyakh Mammoth, already seen from only few species in common (Table 2).

The most abundant moss fragments from the Bykovsky Mammoth scull belong to *Drepanocladus brevifolius*, a species confined to the high latitude tundra areas. Other mire species are also more characteristic for tundra wetlands: *Scorpidium scorpioides, Loeskypnum badium, Calliergon richardsonii, Drepanocladus trifarium*, *Tomentypnum involutum*, *Meesia uluginosa,* and *Orthothecium chryseon*. In more southern parts of Siberia, these species are confined to rich fens and are in general rather rare. The presence of *Encalypta alpina*, *E. procera*, *Tortella splendida, Distichium capillaceum,* and *Flexitrichum flexicaule* also indicates calcium-rich substrates. Northern flora element is represented by *Cyrtomnium hymenophyllum, Polytrichastrum septentrionale*, and also by *Brachythecium tauriscorum*, though the latter specimen is too scarce for certain identification.

General comments on the moss composition in the Bykovsky mammoth scull

The study of the mammoth body is continued by various specialists, and before its completion it would be too early to discuss all details of its burial. All what is quite definite is that mosses with soil were moved inside the scull in a short time after this mammoth has been killed by ancient men. The number of moss species accumulated in its nose cavity appeared to be comparatively high; it is also obvious that they were gathered from a limited area, and therefore their list might by assumed as a kind of relevé.

The combination of mire species listed above and, at the same time, rarity of *Sphagnum* is a characterstic for the tundra-steppe environments in continental areas of Yakutia. The mixture of mire species with rather numerous species of eroded soil (*Distichium, Flexitrichum, Bryum, Totella, Enclypta, Polytrichum, Polytrichastrum*) indicates a mosaic of polygonal tundra with hollows and hummocks, and numerous permafrost ‘frost boils’ and ‘mud circles’. Such combination of species of contrasingly different ecology often appears on eroded soil of thermocarst depressions and pits where the scull of Bykovsky Mammoth was sinking during burial.

A rather high concentration of calcium carbonate is supported by the presence of *Fissidens adianthoides, Cyrtomnium, Didymodon* spp*., Encalypta procera, Meesia uliginosa, Orthothecium,* and *Tomentypnum*. However, the diversity of habitats made possible the occurrence in close proximity of more acidophilous species as well, e.g. *Pleurozium schreberi* that could grow of scattered *Sphagnum* hummocks (cf. Fig. 1C).

The presence of *Leskea* is the most enigmatic; however, it could grow on *Salix* shrubs along brooks and streams (Fig 1D), which agrees with the evaluation of the climate of that epoch being somewhat warver than now (Ukraintseva, 2002).

Acknowledgements

We thank Lars Hedenäs for confirming some problematic identifications of *Scorpidium*. The work of A. Protopopov was carried out with the support of the Russian Science Foundation (grant no. 24-27-20045). The work of Ivanova was supported by IBPC institution projects №АААА-А-21-121012190038-0 and №125102712105-7. The work of M.S. Ignatov and T.V. Voronkova was carried out within the MBG project no. 122042700002-6. The work of E.A. Ignatova was conducted under the state assignment of Lomonosov Moscow State university.

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Received 5 April 2025 *Accepted 15 December 2025*