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A REVISION OF THE *DIDYMODON PEROBTUSUS* GROUP (POTTIACEAE, BRYOPHYTA) IN RUSSIA

К СИСТЕМАТИКЕ МХОВ ГРУППЫ *DIDYMODON PEROBTUSUS* (POTTIACEAE) В РОССИИ

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Abstract

Morphological and molecular phylogenetic studies of two closely related species of *Didymodon, D. perobtusus* and *D. subandreaeoides* were conducted based on collections from Russia. Nuclear ITS based phylogenetic tree found *D. perobtusus* in a maximally supported terminal clade, albeit nested in a grade of *D. subandreaeoides.* The presence of *D. perobtusus* in the Caucasus, Subpolar Urals, Taimyr, Yakutia and Sakhalin Island was not confirmed; thus, its distribution in the country is restricted to southern Siberia, from the Baikal Lake area to the Altai Mts, with one disjunct locality on the eastern macroslope of the Polar Urals. In contrast, *D. subandreaeoides*, which was previously recorded from two localities in Russia, appeared to have wider distribution in Siberia, in areas with calcareous bedrock. An assignment of numerous collections from Yakutia to *D. subandreaeoides* was confirmed by ITS sequences; all these specimens possess both flagelliform innovations with small leaves (main diagnostic character of this species) and clusters of axillary gemmae (not characteristic for this species, only once tentatively mentioned previously) while gemmae were not observed in specimens from Chukotka, Altai and Sayan Mts, Buryatia, Irkutsk Province, and Zabaikalsky Territory. Mature sporophytes of *Didymodon perobtusus* are newly described; they were collected in 2022 in Tunkinsky Nature Park (Republic of Buryatia). Morphological distinctions between *D. perobtusus* and *D. subandreaeoides* are discussed, focusing on the differences in the perichaetial leaves and peristome. *Didymodon nigrescens* is found in collections from Sakhalin; this is the first record of the species from Russia. Descriptions, illustrations, and habitat data are provided for the three species, and distribution maps in Russia are also presented.

Резюме

Проведена ревизия гербарных коллекций двух близкородственных видов из рода *Didymodon, D. perobtusus* и *D. subandreaeoides,* собранных на территории России, с использованием морфологических и молекулярно-генетических методов. Присутствие *D. perobtusus* на Кавказе, Приполярном Урале, Таймыре, в Якутии и на Сахалине не было подтверждено; таким образом, его распространение в России ограничивается югом Сибири, от Байкала до Алтая, с одним дизъюнктивным местонахождением на восточном макросклоне Полярного Урала. В противоположность этому, ареал *D. subandreaeoides*, ранее известного в России только из двух местонахождений, оказался значительно более широким: он выявлен во многих местонахождениях на юге Сибири и в Якутии, в местах, где имеются карбонатные породы. Принадлежность многочисленных коллекций из Якутии к *D. subandreaeoides* подтверждена анализом последовательностей ITS; все эти образцы имеют как флагелловидные веточки с мелкими листьями, считавшиеся главным диагностическим признаком этого вида, так и кластеры выводковых тел в пазухах листьев, которые для этого вида не характерны; однако в образцах *D. subandreaeoides* с Чукотки, Алтая, Саян, из Бурятии, Иркутской области и Забайкальского края выводковые почки обнаружены не были. Впервые описаны спорофиты *Didymodon perobtusus*; они были собраны в 2022 году в Тункинском национальном парке в Бурятии. Обсуждаются морфологические отличия между *D. perobtusus* и *D. subandreaeoides*, подчеркнуты различия в форме перихециальных листьев и перистоме. *Didymodon nigrescens* выявлен в коллекциях с о. Сахалин; он впервые приводится для территории России. Даны описания, иллюстрации и сведения о местообитаниях этих трех видов, а также карта их распространения в России.

KEYWORDS: taxonomy, mosses, molecular phylogeny, nuclear ITS, Siberia, *Didymodon subandreaeoides*, *Didymodon nigrescens*.

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INTRODUCTION

Didymodon perobtusus Broth., *D. subandreaeaoides* (Kindb.) R.H. Zander, and *D. nigrescens* (Mitt.) K. Saito are closely related species sharing such morphological characters as the blackish color of plants, non-keeled leaves, obtuse or blunt leaf apices, crenulate distal leaf margins, thin costae, and stems with a weak or absent central strand. Molecular phylogenetic analysis (Jiménez *et al.*, 2022) placed them in a separate maximally supported clade within *Didymodon* s.str., in a sister position to *D. rigidulus* Hedw. *Didymodon perobtusus* was described from Mongolia (Brotherus, 1928); it is currently known from China (Li *et al.*, 2001) and NW North America (Zander, 2007). In Russia, it was reported from southern Siberia (Bardunov, 1974; Savicz-Lyubitskaya & Smirnova, 1970; Ignatov, 1994; Afonina *et al.*, 2017), Subpolar Urals (Lapshina *et al.*, 2020), Anabar Plateau (Fedosov *et al.*, 2011), Yakutia (Ignatova *et al*., 2018, 2020), Sakhalin (Bakalin *et al.*, 2009), and the Caucasus (Ignatov *et al*., 2010). *Didymodon subandreaeoides* was described from British Columbia and is currently known in NW North America from Alaska, Yukon, Alberta, NW Territories, and Colorado (Zander, 2007). Cao and Gao (1995) in the course of their revision of the genus *Andreaea* Hedw. in China synonymized *Andreaea kashyapii* Dixon ex Vohra & Wadhwa with *D. subandreaeoides*; they provided an illustration of the latter species and circumscribed its distribution in China. However, it was not included in the treatment of *Didymodon* in China by Li *et al.* (2001). Kučera & Köckinger (2000) found that a European taxon *Didymodon rigidulus* subsp. *andreaeoides* (Limpr.) Wijk & Margad. (*Grimmia andreaeoidea* Limpr.) is identical to *D. subandreaeoides*, so the known distribution of this species was considerably expanded, now including the Alps, Carpathians, and mountains in Romania. Later it was recorded by K. Hassel and H.H. Blom from Norway (Ellis *et al.*, 2020). The species was also subsequently reported by Sollman (2005) from the Himalayan Region (Bhutan, China, Kashmir in India and Nepal) and Mongolia; he mentioned one specimen from Nepal with sporophytes, which were unknown before, but did not provide their full description, only mentioning that peristome teeth are straight when wet. This report was, however, doubted by Inoue *et al.* (2020) who discovered *D. subandreaeoides* in collections from Japan, including fruiting specimens, but with eperistomate capsules, even under the opercula. In Russia, *D. subandreaeoides* was recorded for the first time from Chukotka by Afonina (1989). It was known in the country only from localities in Beringian Chukotka (Afonina, 2004; Ignatov *at al.*, 2006) until it was found in one locality from Buryatia (Sofronova *et al*., 2015). In addition, one specimen from Altai Mts (duplicate from MHA, stored as *D. perobtusus*) was mentioned among sequenced samples of *D. subandreaeoides* by Inoue *et al.* (2020) and Jiménez *et al.* (2022). The third species of this group, *D. nigrescens*, was never reported from Russia, though it is known close its boundaries in Japan, as well as it is widely distributed in China. It also occurs in NW North America and penetrates into tropical regions in Africa and Central America (Inoue *et al.*, 2020).

In 2022, the senior author collected several specimens of *Didymodon* with mature sporophytes in Tunka District of Buryatia. They were identified as *D. perobusus*, and sporophytes were previously unknown for this species. At the same time, the record of *D. subandreaeoides* from Altai by Inoue *et al*. (2020) made us suspicious that some other specimens in herbaria may be misidentified. So the aim of the present study was to revise the herbarium collections stored as *D. perobtusus* and *D. subandreaeoides* in LE, MHA and MW in order to clarify their distribution in Russia; some collections, including the specimens with sporophytes, were sampled for molecular study.

MATERIAL AND METHODS

Morphological studies were conducted using traditional methods of light microscopy. Measurements were made under an Olympus CX43 microscope with digital camera Infinity 1-2 and Infinity Analyze software. Illustrations were made under the same microscope with an Olympus drawing tube.

Sequence acquisition

Twelve specimens from Yakutia, Urals, Caucasus and Sakhalin Island identified as *Didymodon perobtusus* were sampled for molecular study. We have chosen an ITS marker, as it was successfully used for delimitation of *Didymodon* species by Inoue *et al*. (2020). The laboratory protocol and sequencing were essentially the same as in our previous moss studies, which are described in detail by Gardiner *et al.* (2005).

Molecular analysis

For comparison three accessions of *D. perobtusus*, nine of *D. subandreaeoides* and seven of *D. nigrescens* were taken from GenBank; six accessions from *D. rigidulus* group, including *D. rigidulus* and *D. validus* Limpr., were used as an outgroup. The tree was rooted on *Geheebia gigantea* (Funck) Boulay. Sequences were aligned using Bioedit (Hall, 1999).

Bayesian analyses were performed in MrBayes 3.2.6 (Ronquist *et al.*, 2012), with 5,000,000 generations, and the chain temperature of 0.02 in all analyses. Convergence of each analysis was evaluated using Tracer1.4.1 (Rambaut *et al*., 2014). Consensus trees were calculated after omitting the first 25% trees as burn-in.

Maximum parsimony analysis was performed in Nona (Goloboff, 1994) in the Winclada shell (Nixon, 1999), with bootstrap calculations for 2000 replications (N searches 100, starting trees per rep 100, max trees 100, do max).

No topological conflict was detected between MP and Bayesian trees, thus only a Bayesian tree is shown in Fig. 1. Bayesian probabilities >0.7 and Bootstrap supports >60% are indicated at branches.

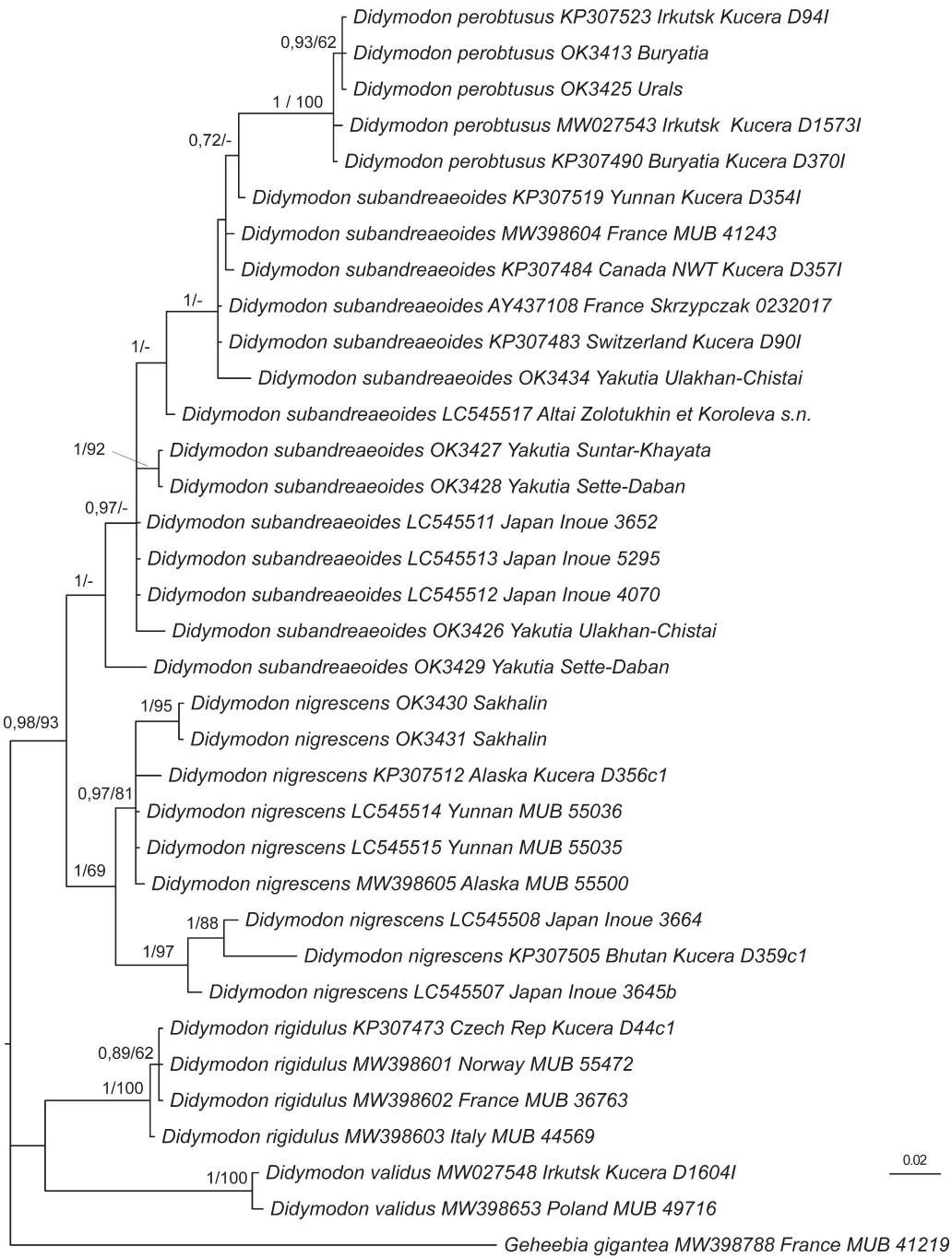

Fig. 1. Bayesian tree of *Didymodon perobtusus*-group inferred from nuclear ITS sequences. Posterior probabilities and / MP bootstrap supports are shown at branches.

Results

DNA analysis

The resulting topology places all accessions of *Didymodon perobtusus*, *D. subandreaeoides,* and *D. nigrescens* into a well-supported clade (0.98/93) sister to the *D. rigidulus* clade. Within this clade, *Didymodon nigrescens* (1/69) and *Didymodon subandreaeoides* + *D. perobtusus* (1/-) are resolved as sister clades. The clade of *D. nigrescens* includes two clades corresponding to 'groups A and B' in the analysis of Inoue *et al*. (2020). Two accessions newly obtained from the specimens from Sakhalin were found within the clade of 'group A', close to accessions from Alaska and Yunnan, thus the first record of *D. nigrescens* in Russia is confirmed.

Five accessions *of D. perobtusus* form a maximally supported clade nested within a grade of *D. subandreaeoides*; it includes two specimens from Buryatia, two from Irkutsk Province, and one from Polar Urals.

One sample from the Dagestan Republic in Caucasus, morphologically referred to as *D. perobtusus,* ap-

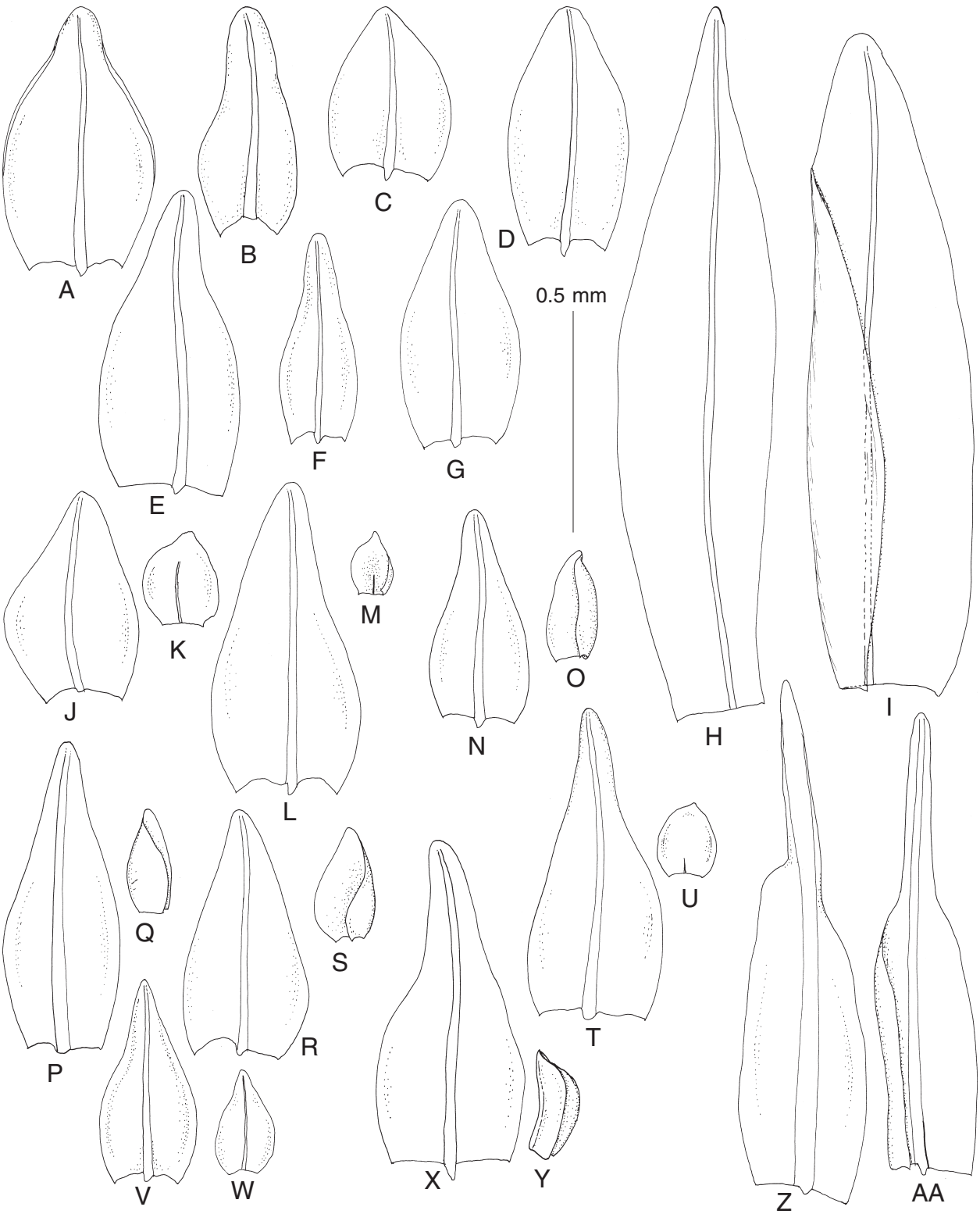

Fig. 2. Leaves of *Didymodon perobtusus* (A-I) and *D. subandreaeoides* (J-AA). A-J, L, N, P, R, T, V: stem leaves; K, M,O, Q, S, U, W, Y: leaves from innovations; H-I, Z-AA: perichaetial leaves. All except 'A' from Russia. A: Mongolia, isotype, LE; B, H-I: Buryatia, Tunka Nature Park, *Afonina 1222*, LE (OK3413); C: Polar Urals, MW9113059 (OK3425); D: Altai, Yaloman, MHA9108774; E: Altai, Teletzkoe Lake, MHA9108775; F: Irkutsk Prov., Slyudyanka, MHA9027582; G: Irkutsk Prov., Slyudyanka, MHA9027410; J-K: Chukotka, MHA9109069; L-M: Altai Mts., Shapshal Range, MHA9108772 (LC545517); N-O: East Sayan Mts., MHA9108778; P-Q, Z: NW Baikal, MHA9108773; R-S, AA: Yakutia, Ulakhan-Chistai Range, MHA9028965 (OK3426); T-U: Yakutia, Suntar-Khayata Range, MHA9021523 (OK3427); V-W: Yakutia, Ulakan-Chistai Range, MW9092629 (OK3434); X-Y: Yakutia, Sette-Daban, MHA9021486 (OK3428). All specimens of *D. subandreaeoides* from Yakutia possess both flagelliform innovations and axillary gemmae. Scale bars: 0.5 mm for all.

peared in the sister position in the *D. nigrescens*-clade (not shown in Fig. 1). However, morphologically it does not fit in this species and will be discussed separately elsewhere.

According to the molecular data, all sequenced specimens from Yakutia which were previously identified as *D. perobtusus* due to the presence of axillary gemmae belong to *D. subandreaeoides*. They are resolved within the polytomy of the latter species represented by accessions from various localities (Europe, North America, Japan, China, Altai Mts in Russia).

Morphological studies

Specimens of *Didymodon nigrescens* from Sakhalin are morphologically similar to the plants from Japan illustrated by Inoue *et al*. (2020) in Fig. 4, belonging to 'group B', and differ from plants of 'group A' shown in Fig 3 in the same paper by wider leaf acumina. However, molecular phylogenetic analysis places them into the clade of 'group A'. Plants from Sakhalin are described and illustrated below.

Morphological study of the sequenced specimen of *Didymodon subandreaeoides* from Altai Mts confirmed that it fits well within the description of this species. It possesses 'normal' shoots with ovate to ovate-lanceolate leaves and flagelliform innovations with small, cochleariform leaves. We found some additional specimens with dimorphic leaves and no axillary gemmae in Sayan Mts, NW Baikal Lake area and Kodar Range in Zabaikalsky Territory (see specimens examined below). Specimens from Chukotka also fit *D. subandreaeoides* in morphology, but they differ from all other specimens by having small leaves from innovations with dentate margins (see the description and illustration below). The most intriguing is the presence of both flagelliform innovations and axillary gemmae in specimens from Yakutia; their identity was confirmed by molecular analysis. All specimens from Yakutia and one specimen from Tokinsky Stanovik in Amur Province are referred to *D. subandreaeoides* as they all possess this combination of characters.

Specimens from the Anabar Plateau (north of Krasnoyarsk Territory) were not sampled for molecular analysis as they were reidentified as *Molendoa hornschuchiana* (Hook.) Lindb. ex Limpr. s.l. (*M. tenuinervis*-morphotype). A specimen from Khulga River valley (Subpolar Urals) which was reported as *D. perobtusus* (Sofronova *et al*., 2015) also belongs to *Molendoa hornschuchiana* s.l.

Sporophytes are newly described for *D. perobtusus* below. Fertile plants were recently collected by the senior author in one locality in Buryatia. The identity of this specimen is confirmed by molecular data (isolate 3413). Its capsules have peristome (see the description below), while capsules of *D. subandreaeoides* were described as eperistomate by Inoue *et al.* (2020) who found fertile specimens of this species in Japan. However, each of these two species was collected with sporophytes only once. Some difference in the shape of perichaetial leaves between these two species was also observed (cf. Fig. 2H-I and Z-AA), though it was shown on a limited number of specimens. We refer to *D. perobtusus* all specimens with clusters of axillary gemmae but no innovations with cochleariform leaves.

Discussion

The results of the molecular analysis call for a revaluation of morphological distinctions between *Didymodon perobtusus* and *D. subandreaeoides*. These species were usually separated mainly by the constant presence of unicellular gemmae born in clusters in leaf axils in the former species and dimorphic leaves in the latter species (Zander, 2007). A comparison between them was provided only in the Flora of North America, because both species occur there in the north-west of the continent. In China, where both species also occur, only *D. perobtusus* was included into the treatment by Li *et al*. (2001). In the treatment of *Barbula* (including *Didymodon*) for Russia (Savicz-Lyubitzkaya & Smirnova, 1970), only a single specimen of *D. subandreaeoides* collected by L.V. Bardunov in the NW Baikal Lake area (originally identified by Bardunov as *Didymodon rigidulus* subsp. *andreaeoides*) was discussed. It was referred to *D. perobtusus,* though axillary gemmae were not mentioned (we did not observe them in this specimen). Since the assignment of Yakutian specimens with axillary gemmae to *D. subandreaeoides* is confirmed, it makes morphological identification of both species more difficult. Such plants were also mentioned by Kučera & Köckinger (2000) who wrote that the specimen "from Clogwyn du'r Arddu (Wales, U.K.) … is in habit and anatomical and morphological details identical to *D. subandreaeoides* but its numerous axillary gemmae of *Didymodon rigidulus*-type do not fit its known variability". So, the presence of flagelliform innovations with small leaves remains the only reliable morphological character that helps to distinguish sterile specimens of *S. subandreaeoides* from *D. perobtusus*. Our attempts to separate these species by leaf shape and size have failed because these characters are highly variable in both species (see Fig. 2). These facts, as well as the nested position of *D. perobtusus*-clade in *D. subandreaeoides* may even suggest merging of *D. perobtusus* within the latter species. However, the clade of *D. perobtusus* is maximally supported, thus providing an evidence of its separate status; furthermore, there is an obvious difference between peristomate capsules of *D. perobtusus* and those lacking peristome of *D. subandreaeoides* (cf. Inoue *et al*., 2020). Plants with sporophytes are extremely rare in both species, but female plants with archegonia are occasionally seen in herbarium collections; the difference in shape of perichaetial leaves (cf. Fig. 2H-I and Z-AA) may also be taken into account as an additional distinction (however, with some caution, since this character was studied in a limited number of specimens).

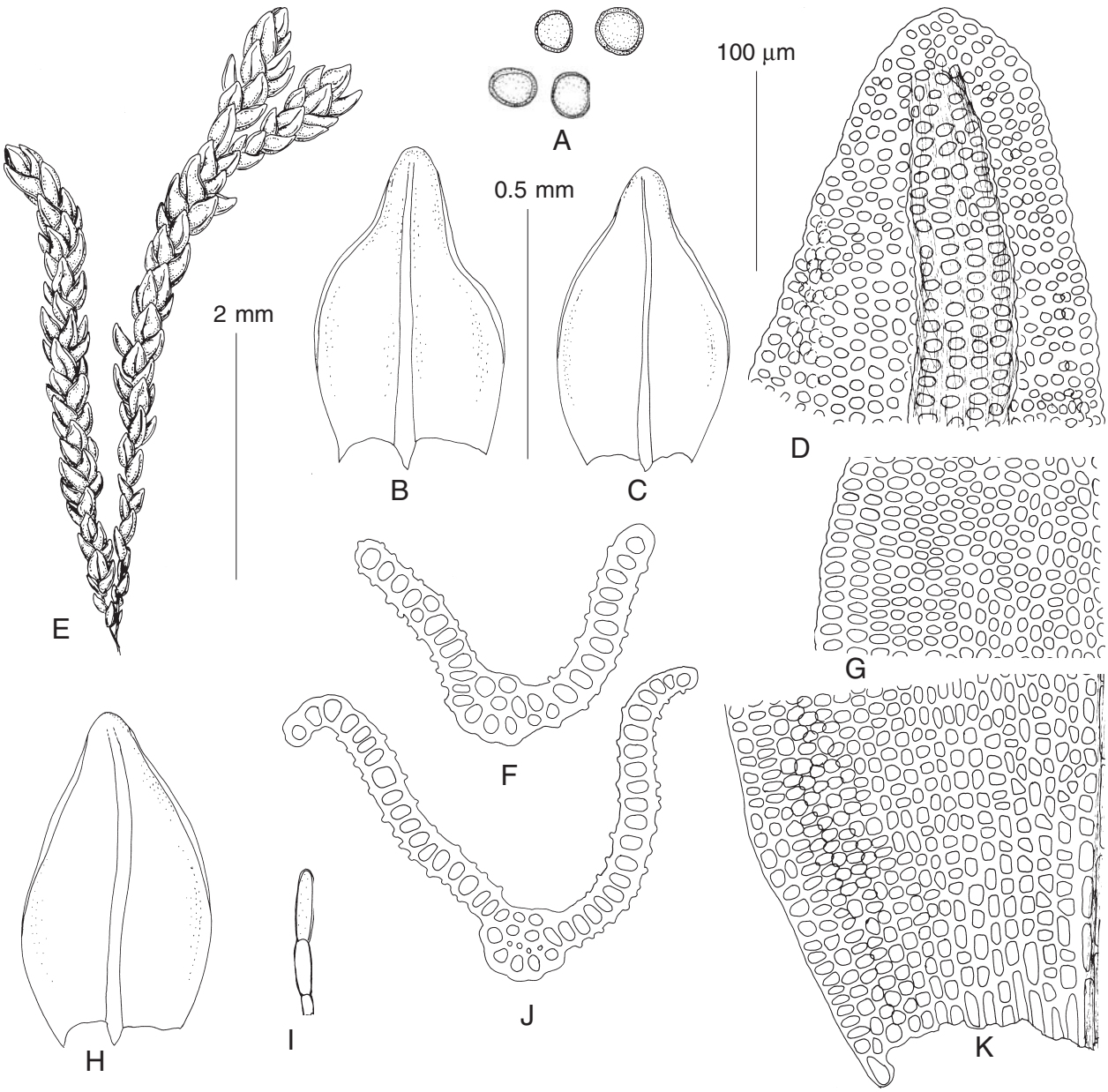

Fig. 3. *Didymodon perobtusus* (from syntype). A: gemmae; B-C, H: leaves; D: upper leaf cells; E: habit, dry; F, J: leaf transverse sections; G: mid-leaf cells; I: axillary hair; K: basal leaf cells. Scale bars: 2 mm for E; 1 mm for B-C, H; 100 μm for D, F–G, I-K.

TAXONOMY

Didymodon perobtusus Broth., Rev. Bryol., n.s. 2: 1. 1928. — *Barbula perobtusa* (Broth.) P.C. Chen, Hedwigia 80: 194. 28 f. 1–5. 1941. Figs. 3-5, 2A-I, 10

Plants in low, dense tufts, dark brown to black, dull. *Stems* 3–6 mm, sparsely branched, hyalodermis absent, cortical cells in 1–2 rows, medullar cells in 2–3 rows, ± thick-walled, central strand narrow or well-developed. *Leaves* loosely to tightly appressed when dry, erect when moist, the middle part of stems 0.3–0.5×0.15–0.25 mm, upper and subperichaetial leaves 0.6–1.0×0.3–0.4 mm, ovate to ovate-lanceolate, gradually tapered to apex or with shoulders, rounded-obtuse at apex, concave, not keeled distally; margins plane or widely recurved in mid-leaf, crenulate distally; costa thin, ca. 20–25 μm wide at base, not narrowed distally, ending a few cells before apex, semicircular in transverse section, with 2 guide cells, ventral and dorsal epidermis and 0–1 layered dorsal stereid band; laminal cells thick-walled, upper and middle laminal cells round or transversely ovate, 5–15×7–10 μm, papillose, papillae simple, 1–2 per cell, or smooth; basal juxtacostal cells quadrate to short rectangular, 10–20×8–11 μm, smooth, basal marginal cells in several rows rounded-quadrate, ovate or transversely ovate. *Specialized vegetative reproduction* by 1(2)-celled gemmae 17–23 μm in diameter, born in clusters in leaf axils. *Dioicous*, sporophytes rare. *Male plants* smaller than female, with several perigonia per stem. Perigonial leaves wide-

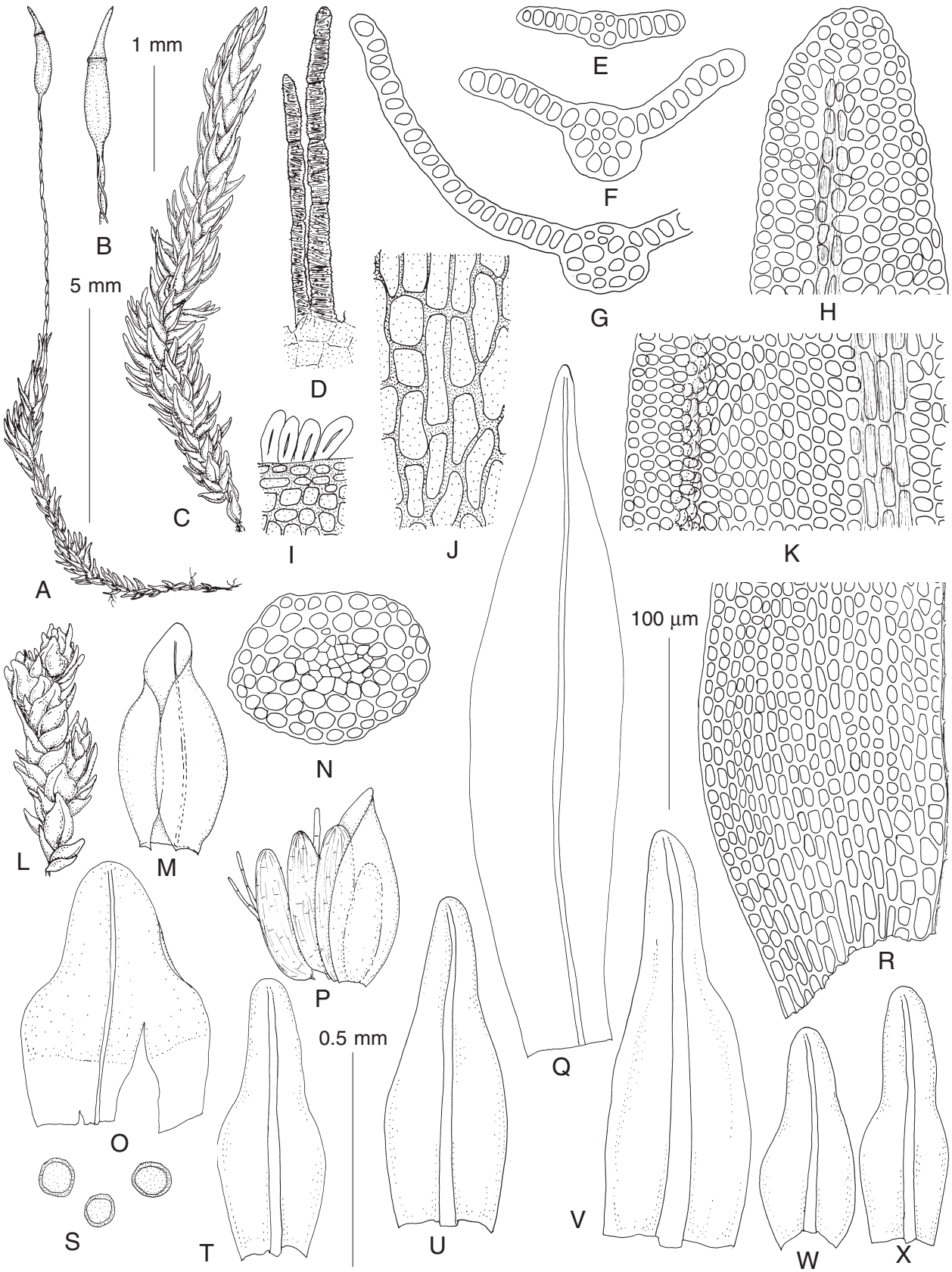

Fig. 4. *Didymodon perobtusus* (from: Russia, Buryatia, Tunka Nature Park, *Afonina 1222*, LE). A: plant with sporophyte, dry; B: capsule; C: sterile plant, wet; D: part of peristome; E–G: leaf transverse sections; H: upper leaf cells; I: annulus; J: exothecium; K: mid-leaf cells; L: male plant, wet; M, O: perigonial leaves; N: stem transverse section: P: part of perigonium; Q: inner perichaetial leaf; R: basal leaf cells; S: gemmae; T–X: leaves. Scale bars: 5 mm for A; 1 mm for B–C, L; 0.5 mm for M, O–Q, T–X; 100 µm for D–K, N, R.

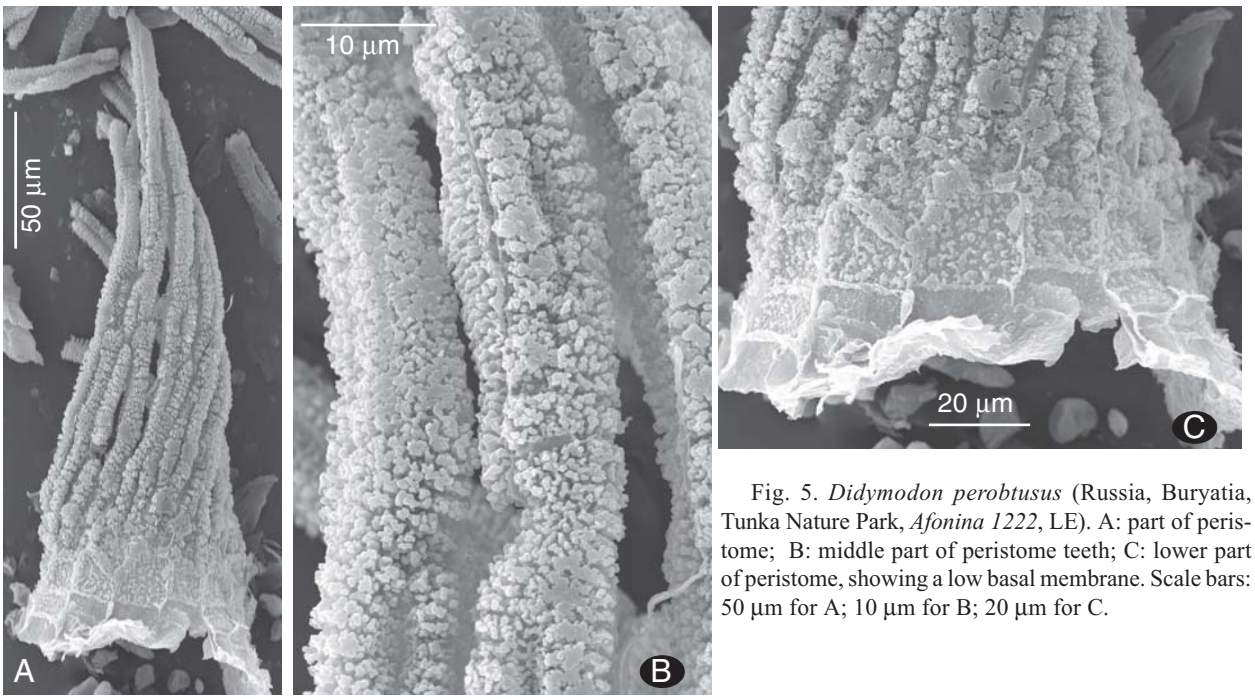

Fig. 5. *Didymodon perobtusus* (Russia, Buryatia, Tunka Nature Park, *Afonina 1222*, LE). A: part of peristome; B: middle part of peristome teeth; C: lower part of peristome, showing a low basal membrane. Scale bars: 50 µm for A; 10 µm for B; 20 µm for C.

ly ovate, strongly concave, rounded at apex, with hyaline basal part. *Perichaetial leaves* 1.2–1.4×0.3–0.4 mm, oblong-lanceolate, gradually tapered to apex. *Setae* ca. 4 mm, reddish-brown, flattened and spirally twisted when dry. *Urn* cylindrical, 0.8 mm long, 0.2 mm wide, gradually narrowed to the mouth, dark cherry-red, smooth. *Annulus* deciduous. *Operculum* long rostrate, ca. 0.6 mm long. *Peristome teeth* slightly twisted when dry, straight when wet, 130–170 mm long, horizontally striolate and finely papillose. *Spores* 9–11 µm.

Distribution and ecology. In Russia *Didymodon perobtusus* occurs in the mountainous areas of southern Siberia. It is most frequent in the East Sayan Mts and is known from several localities in NE surroundings of Baikal Lake, Transbaikalia, Tyva Republic, and Altai Mts. It was also collected on limestone massif Yanganape on eastern slope of Polar Urals. It occurs in altitude range 600–2300 m, growing on base-rich rock outcrops on slopes and on river banks, on rocky slopes, on wet cliffs and rocks near waterfalls.

Differentiation. *Didymodon perobtusus* differs from most species of *Didymodon* by having dark-brown color of plants, ovate leaves with crenulate upper margins, and mostly unicellular axillary gemmae. Its distinction from the similar *D. subandreaeoides* is discussed under that species. It can be also confused with *Bryoerythrophyllum inaequalifolium* (Taylor) R.H. Zander, which has similar leaf shape and unicellular gemmae. The latter species differs in having leaves with more strongly recurved margins, densely papillose laminal cells, with c-shaped papillae, and costae with two well-developed stereid bands.

Specimens examined: MONGOLIA: Kosogol [Khubsugul] Lake, 27 July 1902 *Elenkin* (LE) (Syntype). RUSSIA: **Yamalo-Nentzky Autonomous District:** Eastern slope of Polar Urals, Yanganape limestone massif, *Fedosov 17-1005*, MW9113061. **Altai Republic**: Ongudai Distr., Maly Yaloman Creek, 31 July 1991 *Ignatov & Ignatova 25/170*, MHA9108774; Teletzkoe Lake, Izvestkovaya Mt., 12 July 1989 *Ignatov s.n.*, MHA9108775. **Irkutsk Province:** Slyudyanka Distr., Slyudyanka River valley, right bank, *Ignatov et al. 18-4503*, MHA9027592; same place, left bank, *Ignatov et al. 18-4620,* MHA9027423. **Zabaikalsky Territory:** Kalar District, Kodar Range: Valley of Syulban River, left bank of Khadatkan River, 22 June 2015 *Afonina 3215*, LE B-0039664; Priargynsky District, Byrka Settl., 30 June1989 *Bardunov s.n.,* LE B-0039680. **Republic of Buryatia:** East Sayan Mts: Okinsky District, East Sayan Mts.: valley of Belyi Irkut River, 12 July 2015 *Afonina 1615*, LE B-0039682; Upper of Oka River, Dodo-Zhahna village, 10 km NE of Orlik Settlement, 2 July2008 *Afonina 00708*, LE B-0039691; Upper Oka River, valley of Sorok River, 7 July 2008 *Afonina 02208*, LE B-0039673; same place, 10 July 2008, *Afonina & Tubanova* (Bryophyta Rossica et Civitatum Collimitanearum Exsiccata, Fasc. VIII, №296), LE B-0039694; same place, 7 July 2008 *Afonina 02108*, LE B-0039688; same place, 10.07.2008 *Afonina 03608*, LE B-0039680, LE B-0039681; Valley of Oka River, Zambbolok Creek, Sailag waterfall, *Afonina s.n.*, LE B-0039704; Tunkinsky National Park, mouth of Bugovek River (right tributary of Irkut River), *Afonina 1222*, LE B-0039699; Tunka Distr., Mondy, 24 Aug 1960 *Bardunov s.n.*, LE B-0039677; Tunka Range, Khubuta River, 3 Aug 1960 *Bardunov s.n.*, LE B-0039678.

Didymodon subandreaeoides (Kindb.) R.H. Zander, Phytologia 41: 23. 1978. —*Barbula subandreaeoides* Kindb., Rev. Bryol. 32: 36. 1905. — *Barbula andreaeoides* Kindb., Rev. Bryol. 32: 36. 1905. — *Grimmia andreaeoides* Limpr., Laubm. Deutschl. 1: 776. 1889.

Figs. 6-8, 2J-AA, 10.

Plants in low, dense tufts, dark brown to black, dull green at shoot tips. *Stems* 5–8 mm, sparsely branched,

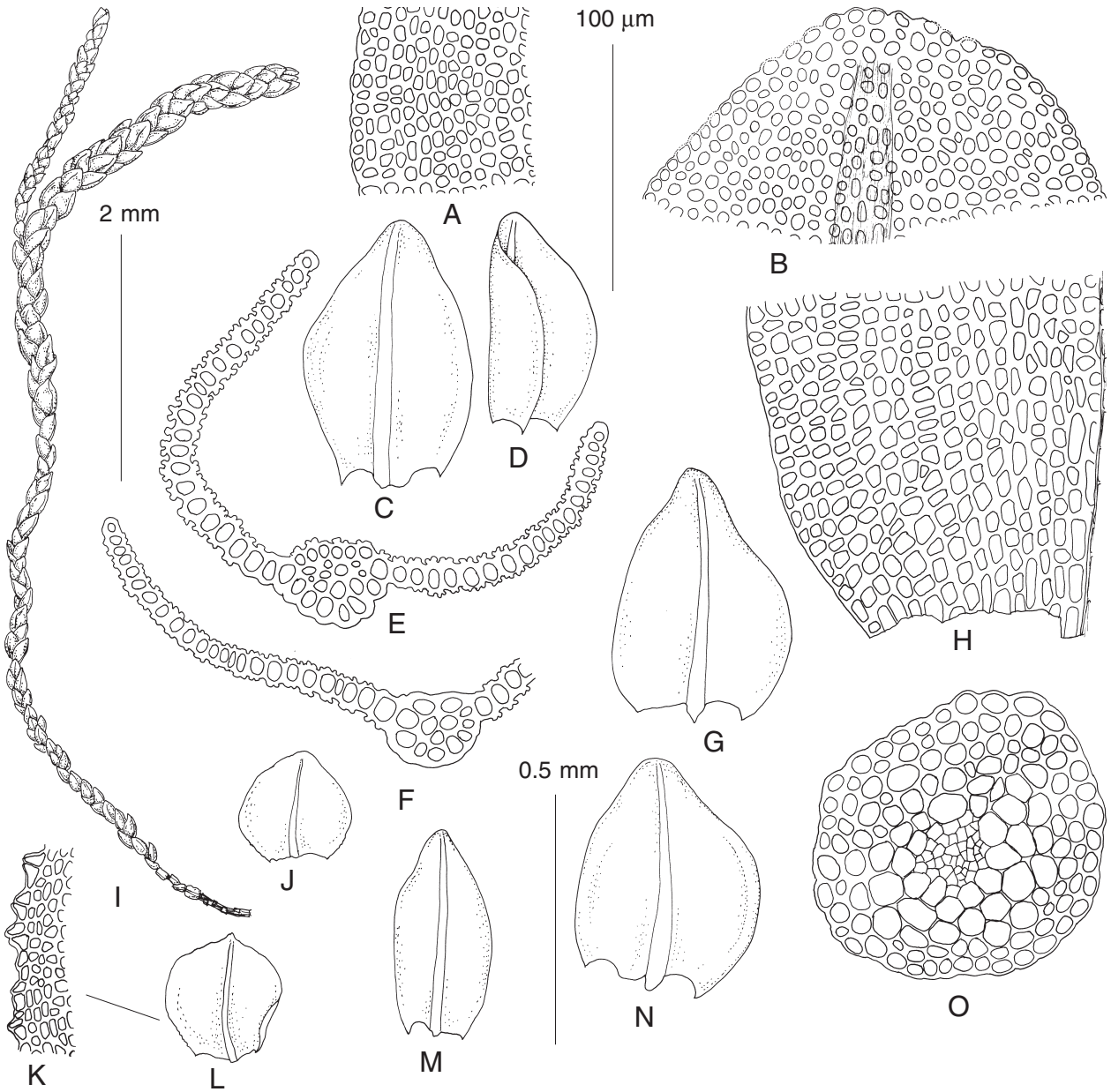

Fig. 6. *Didymodon subandreaeoides* (from: Russia, Chukotka, 2 Sept 1975, *Afonina s.n.*, MHA9109069). A: mid-leaf cells; B: upper leaf cells; C–D, G, M–N: stem leaves; E–F: leaf transverse sections; H: basal leaf cells; I: habit, dry; J, L: leaves from innovations; K: basal marginal cells of innovation leaf; O: stem transverse section. Scale bars: 2 mm for I; 0.5 mm for C–D, G, M–N; 100 µm for A–B, E–F, H, K, O.

hyalodermis absent, cortical cells in 1–2 rows, medullar cells in 1–2 rows, thick-walled, central strand narrow or absent; flagelliform innovations with small, cochleariform leaves always present, scarce to numerous. *Leaves* on main stems loosely to tightly appressed when dry, erect when moist, 0.35–0.55×0.25–0.4 mm, ovate to ovate-lanceolate, gradually tapered to apex, rarely with shoulders, rounded-obtuse at apex, concave, not keeled distally; margins plane or widely recurved in midleaf; costa thin, ca. 20 µm wide at base, not narrowed distally, ending few cells before apex, semicircular in transverse section, with 2 guide cells, ventral and dorsal epidermis, 1–2 rows of substereids between guide cells and dorsal epidermis; laminal cells thick-walled, upper and middle laminal cells round or transversely ovate, 7–16×7–12 µm, papillose, papillae low, branched, 1–2 per cell, basal juxtacostal cells 10–20×8–11 µm, smooth, basal marginal cells in several rows round, transversely ovate or ovate. *Leaves from flagelliform innovations* 0.20–0.25×0.18–0.23 µm, round to widely ovate, strongly concave, costa single, ending below apex or short, occasionally absent; margins entire or, in specimens from Chukotka, with 'double' teeth formed by protruding lower angle of upper cell and upper angle of adjacent lower cell. *Specialized vegetative reproduction* absent or present (in specimens from Yakutia and north of Amur Province), by 1(2)-celled gem-

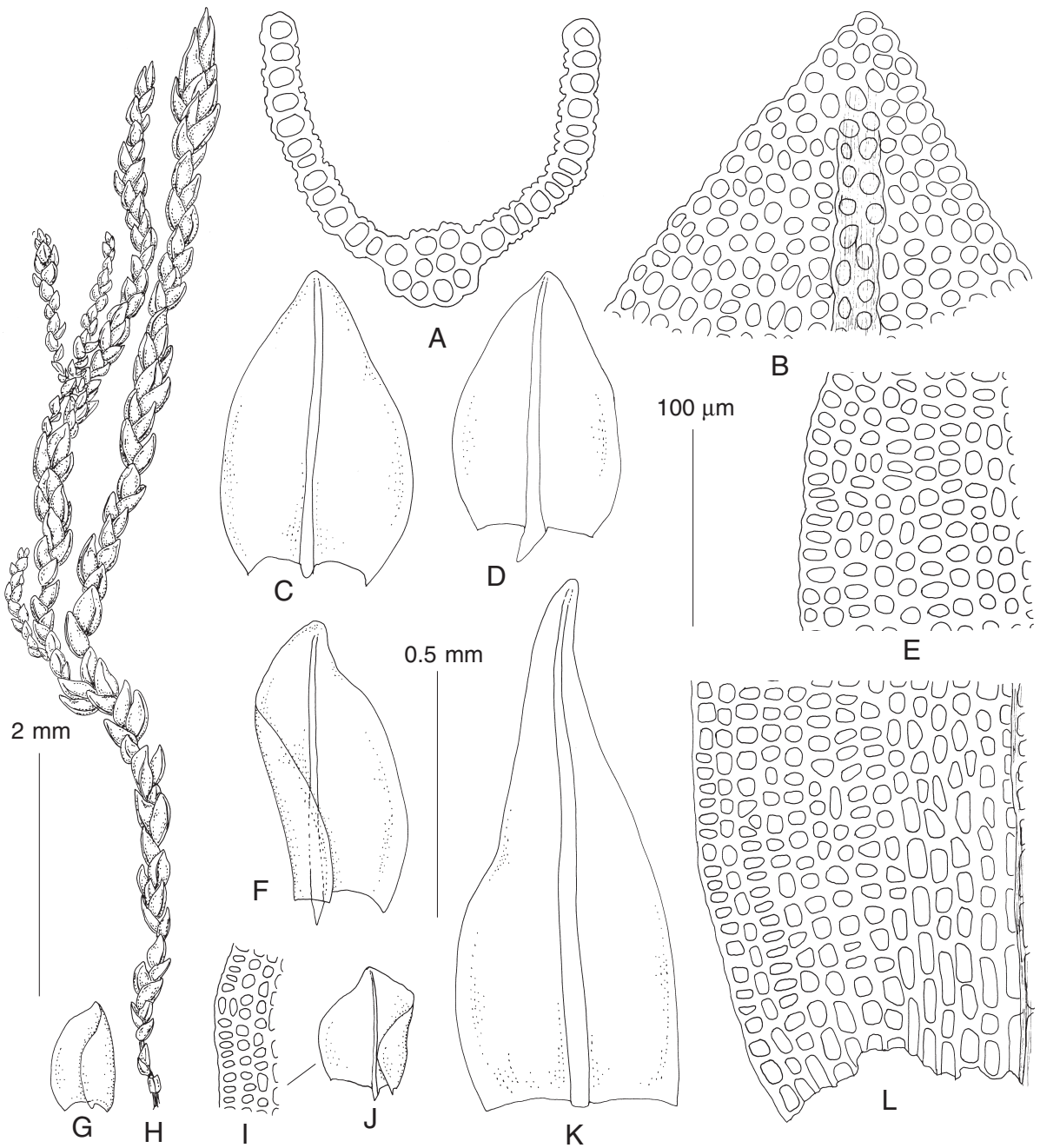

Fig. 7. *Didymodon subandreaeoides* (from: Russia, Altai Mts, 15 July 1990, *Zolotukhin & Korolyeva s.n.*, MHA9108772). A: leaf transverse section; B: upper leaf cells; C–D, F: stem leaves; E: mid-leaf cells; G, J: leaves from innovations; H: habit, dry; I: basal marginal cells of innovation leaf; K: perichaetial leaf; L: basal leaf cells. Scale bars: 2 mm for H; 0.5 mm for C–D, F–G, J–K; 100 µm for A–B, E, I, L.

mae 17–23 µm in diameter, born in clusters in leaf axils. *Dioicous*, female plants with archegonia occasionally present, male plants not seen. Sporophytes unknown in Russia. [Capsules eperistomate (cf. Inoue *et al.*, 2020)].

Distribution and ecology. Like *Didymodon perobtusus, D. subandreaoides* occurs in Russia in southern Siberia from Altai to Buryatia and Transbaikalia; it was also found in several localities in Yakutia: Sette Daban, Suntar-Khayata and Ulakhan-Chistai Mt. Ranges, and in Beringian Chukotka. It is also known from single locality in Tokinsky Stanovik Range (Amur Province). The species grows at low altitudes in Chukotka and Yakutia, 50–1000 m a.s.l., while in the mountains of southern Siberia it was found between 1200 and 1700 m. It occurs in arctic and mountain tundra of forb-sedge type, on rock outcrops in moss-lichen community, on boulders in larch forest, on rocky banks of creeks and rivers, on wet limestone cliffs near waterfalls and in places with dripping water (melting permafrost), in Yakutia occasionally in places where *Andreaeobryum macrosporum* Steere & B.M. Murray was collected.

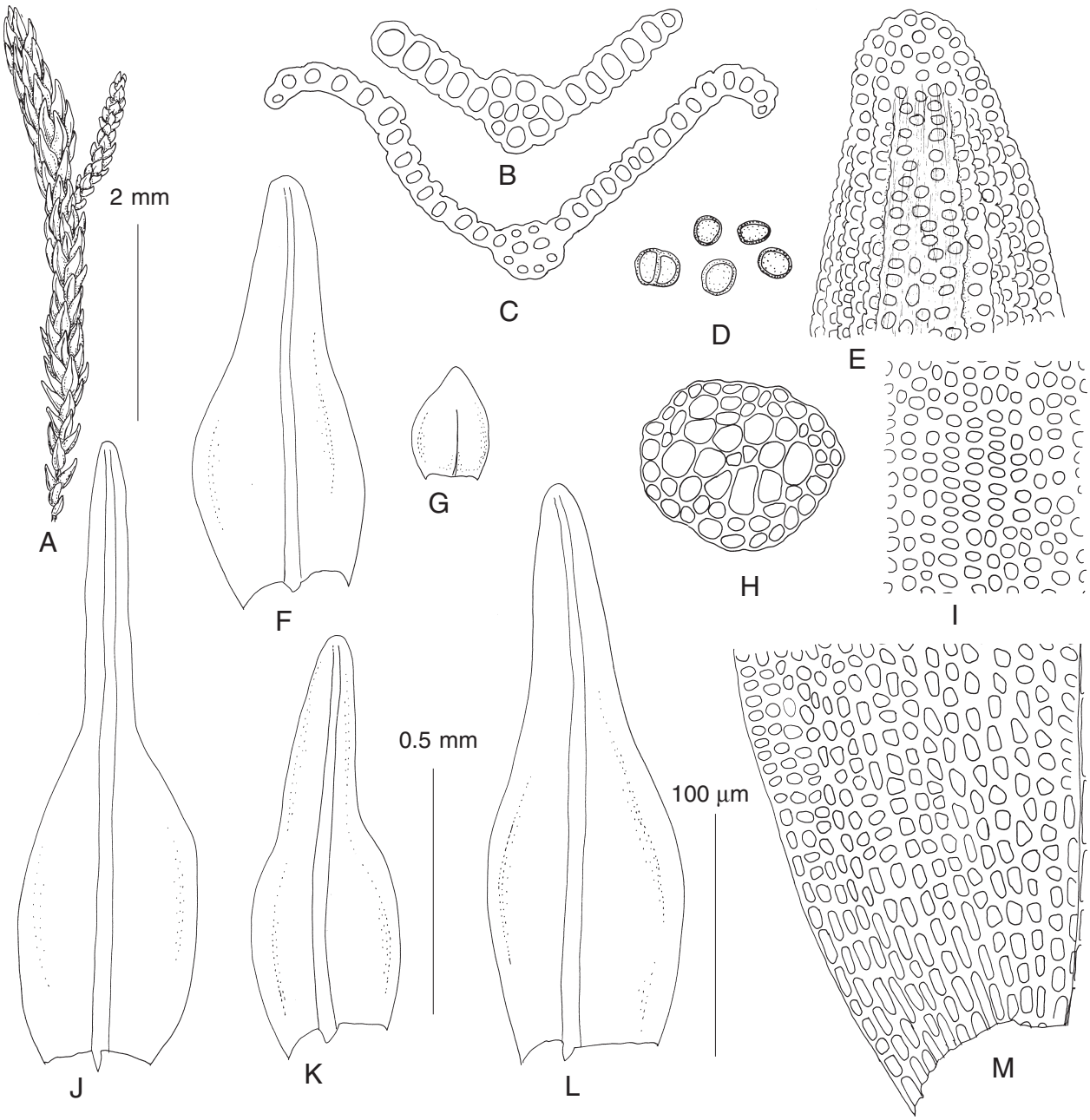

Fig. 8. *Didymodon subandreaeoides* (from: Russia, Yakutia, Sette Daban Range, *Ivanov 17-605*, MHA9027661). A: habit, dry; B–C: leaf transverse sections; D: gemmae; E: upper leaf cells; F, K: lower stem leaves; G: leaf from innovation; H: stem transverse section; I: mid-leaf cells; J: perichaetial leaf; L: subperiachaetial leaf; M: basal leaf cells. Scale bars: 2 mm for A; 0.5 mm for F–G, J–L; 100 µm for B–E, H–I, M.

Differentiation. *Didymodon subandreaeoides* is very similar to *D. perobtusus* in plant color, leaf shape, crenulate upper leaf margins, and thick-walled, papillose laminal cells; it even possesses unicellular axillary gemmae in some populations. However, the presence of innovations with small, strongly concave leaves is a unique feature of *D. subandreaeoides*. It also separates this species from similar species of *Didymodon* and other genera of the Pottiaceae.

Specimens examined: RUSSIA: **Chukotka:** Lavrentiy Bay, Krauze Cape, 2 Sept 1975. *Afonina s.n.,* LE B-0039663; Chegitun' River basin, 24 July1972 *Razzhivin s.n.*, LE B-0039662; same place, 1 km upstream from Putukuneiveem River mouth, 24 July 2003, *Razzhivin s.n.*, LE B-0039661. **Republic of Sakha/Yakutia:** Momsky Distr., Ulakhan-Chistai Mt. Range, western foothill of Mramornaya Mt., *Ignatov & Ignatova 18-1360*, MW9091288; same place, 930 m alt., *Ignatov & Ignatova 18-1815*, MHA9029531; Pravy Dzhapkychan Creek, *Ignatov & Ignatova 18-2712*, MHA9028794; Tomponsky Distr.: left bank of Vostochnaya Khandyga River opposite Segenyakh Creek moutyh, *Ivanov 17-729*, MHA9027663; Sette Daban Range, right slope of Vostochnaya Khandyga River valley between Shaman and Segenyakh Creeks, *Ignatov & Ignatova 16-1563*, MHA9021499; same place, Shaman Creek, *Ignatov & Ignatova 17-32*, MHA90256925. **Republic of Buryatia:** Okinsky

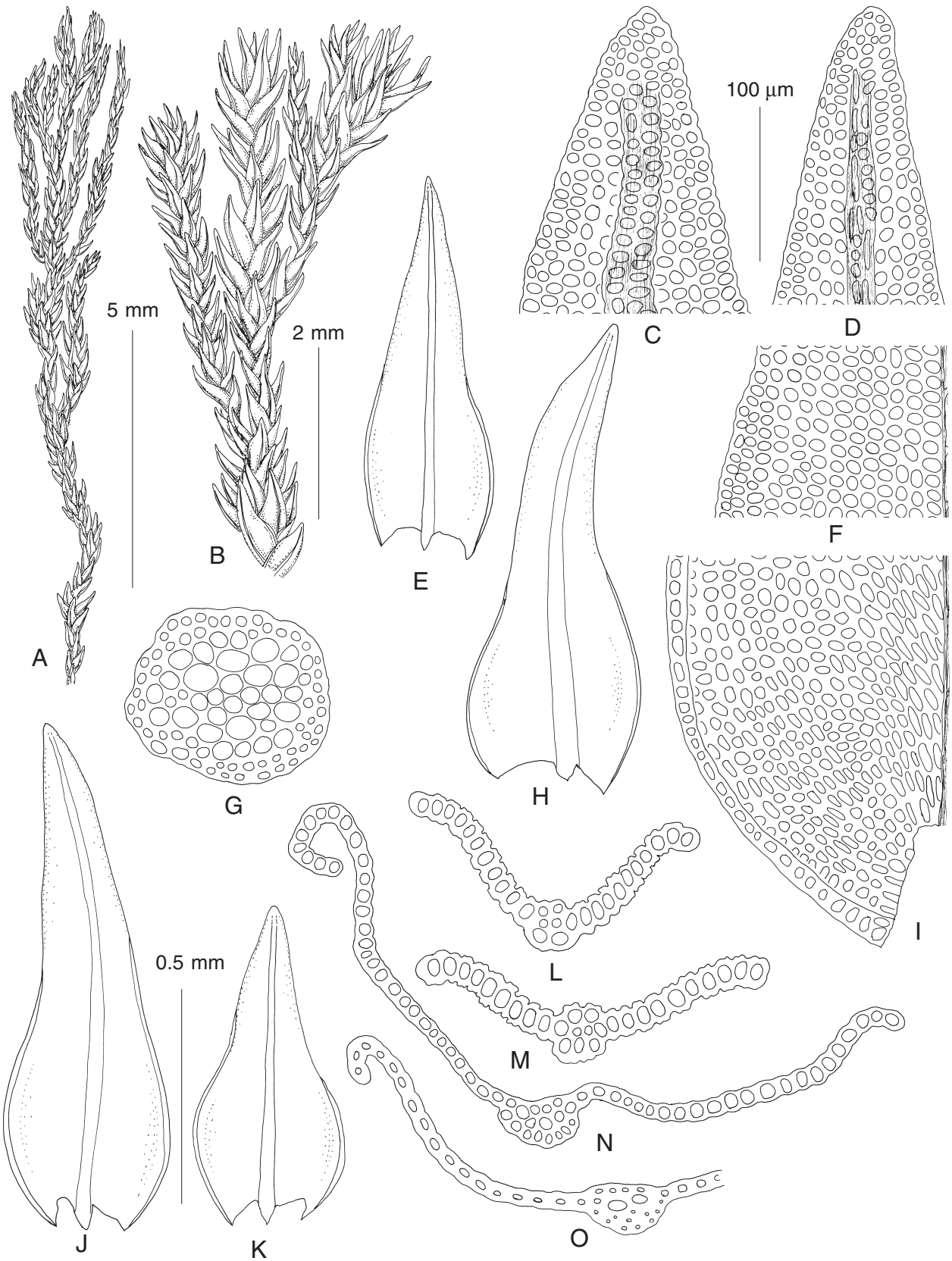

Fig. 9. *Didymodon nigrescens* (from: Russia, Sakhalin Island, *Ignatov & Teleganova 06-3543*, MW9036033). A: habit, dry; B: habit, wet; C–D: upper leaf cells; E–H, J–K: stem leaves; F: mid-leaf cells; G: stem transverse section; I: basal leaf cells; L–O: leaf transverse sections. Scale bars: 2 mm for H; 0.5 mm for C–D, F–G, J–K; 100 µm for A–B, E, I, L.

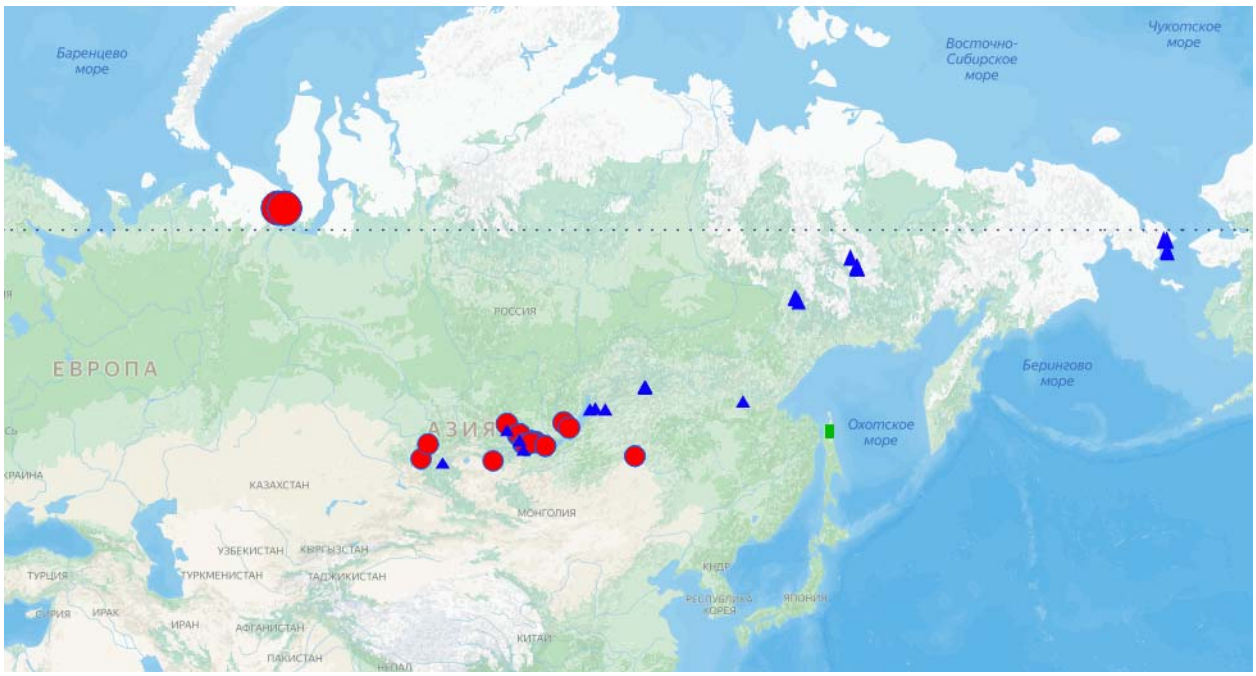

Fig. 10. Distribution of *Didymodon perobtusus* (circles), *D. subandreaeoides* (triangles) and *D. nigrescens* (rectangle) in Russia.

District, East Sayan Mts.: upper of Oka River, Valley of Sorok River, alt. 1755 m, 9 July 2008 *Afonina 03008*, LE B-0039657; Okinsky District, East Sayan Mts, Valley of Belyi Irkut River, 12 July 2015 *Afonina 1715*, LE B-0039656; Kurumkan District, Dzherginskiy State Reserve. Upper Barguzin River, 1 Aug 2013 *Mamontov YuSM-386-1*, LE B-0039659 & LE B-0039660; NE Baikal, Tompuda River, 19 Aug 1956 *Bardunov s.n.*, LE B-0039658; East Sayan Mts, Kadyr-Os River near Chuglyma Creek mouth, 13 July 1961, *Bardunov s.n.*, MHA9108778. **ZABAIKALSKY TERRITORY**: Kalar District, Kodar Range: Levyi Syulban River, 10 June 2015 *Afonina 0715*, LE B-0039665; Syulban River, Zolotoi Klyuch Creek, 12 July 2015 *Afonina 0915/1, 0915/2 & 0915/3*, LE B-0039666, LE B-0039669, LE B-0039670; same place, 13 June 2015 *Afonina 1515*, LE B-0039667; Kalar District, Kodar Range: Valley of Syulban River, left bank of Khadatkan River, 22 June 2015 *Afonina 3215*, LE B-0039668; valley of Syulban River, upper of Oleniy Rog Creek, 16.06.2015 *Mamontov 536/2b*, LE B-0039671; **AMUR PROVINCE**: Zeya Distr., Stanovoy Ridge, Tokinsky-Stanovoy National Park, vicinity of the Tas-Balagan pass, *Dudov TSMF005*, MW9092493.

Didymodon nigrescens (Mitt.) K. Saito, J. Hattori Bot. Lab. 39: 510. 1975. — *Barbula nigrescens* Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1: 36. 1859. Figs. 8-9

Plants rigid, in dense tufts, dark brown, occasionally green at tips, dull. *Stems* 10–25 mm, repeatedly branched; hyalodermis absent, cortical cells in 1–2 rows, medullar cells in 3–4 rows, thick-walled, central strand absent. *Leaves* appressed when dry, erect when moist, in lower and middle parts of stems 0.5–0.7×0.3–0.4 mm, upper leaves to 1.0×0.4 mm, from ovate bases ± abruptly narrowed into triangular acumina, subobtuse at apex, concave, not keeled distally; margins narrowly recurved from base to midleaf; *costa* moderately thick, ca. 40 µm wide at base, not or slightly narrowed distally, subpercurrent, semicircular in transverse section, with two guide cells, dorsal and ventral epidermis, dorsal stereid band absent or 1-layered in lowermost portion of costa; *cells* thick-walled, upper and middle laminal cells 8–11×8–15 µm, papillose, papillae low, branched, 1–2 per cell; basal juxtacostal cells ovate, 10–25×8–11 µm, smooth, in upper leaves in oblique rows, basal marginal cells shorter, ovate to transversely ovate. *Specialized vegetative reproduction* absent. *Dioicous,* only plants with archegonia were seen. *Sporophytes* unknown in Russia.

Ecology. The species was collected on one locality on Sakhalin Island, at the top of low calcareous ridge, in crevices and on surfaces of dry cliffs.

Specimens examined: RUSSIA: Sakhalinskaya Province, Sakhalin Island, Smirnykh Distr., Nature Reserve "Vaida Mountain", 900 m alt., *Ignatov & Teleganova 06-3543*, MW9036033; same place, 920 m alt., *Ignatov & Teleganova 06-3544*, MW9036034.

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Appendix: Voucher specimens and GenBank accessions of *Didymodon*.

D. perobtusus OK3413 Russia, Buryatia, *Afonina 1222* LE B-0039699	OP991893
D. perobtusus OK3425 Russua, Yamal-Nenetz Autonomous District, *Fedosov 17-1007*, MW9113059	OP991894
D. subandreaeoides OK3426 Russia, Yakutia, Ulakhan-Chistai Mts, *Ignatov & Ignatova 18-2176*, MHA9028965	OP991895
D. subandreaeoides OK3427 Russia, Yakutia, Suntar-Khayata Mts, *Ignatov & Ignatova 16-1452*, MHA9021523	OP991896
D. subandreaeoides OK3428 Russia, Yakutia, Sette-Daban Mts, *Ignatov & Ignatova 16-1526*, MHA9021486	OP991897
D. subandreaeoides OK3429 Russia, Yakutia, Sette-Daban Mts, *Ivanov 17-605*, MHA9027661	OP991898
D. nigrescens OK3430 Russia, Sakhalin, *Ignatov & Teleganova 06-3543*, MW9036033	OP991899
D. nigrescens OK3431 Russia, Sakhalin, *Ignatov & Teleganova 06-3544*, MW9036034	OP991900
D. subandreaeoides OK3434 Russia, Yakutia, Ulakhan-Chistai Mts, *Ignatov & Ignatova 18-2712*, MW9091629	OP991901

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