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ON THE GENUS *DIDYMODON* S. STR. (POTTIACEAE, BRYOPHYTA) IN RUSSIA

О РОДЕ *DIDYMODON* S. STR. (POTTIACEAE, BRYOPHYTA) В РОССИИ

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Abstract

The present study addresses problematic groups within *Didymodon* s. str. occurring in Russia, mainly related to *D. validus*, *D. icmadophilus* and *D. acutus*. A combined morphological and molecular-phylogenetic approach revealed that *D. validus* is the commonest species of this group in Russia, especially in its Asian part and the Caucasus, whereas distribution of *D. icmadophilus* is likely restricted to the humid habitats in the Caucasus, and we failed to confirm the identity of any *D. acutus* specimen from the country. *Didymodon cordatus* is sporadically distributed in southern Siberia, Far East and the Caucasus. Four species recently described from China were revealed in Asian Russia: *D. hengduanensis* in Primorsky Territory and Irkutsk Province; *D. daqingii* in southern Siberia and Yakutia; *D. tibeticus* in Zabaikalsky Territory, and *D. mongolicus* in southern Siberia, Yakutia and the Caucasus. However, we failed to find *D. schensianus* which is widespread in neighboring territories of China and Japan. Six species are described as new for science: *D. baicalensis* (Irkutsk Province, Buryatia, Zabaikalsky Territory, Khakassia, Altai Republic), *D. borealis* (Yakutia, Perm Territory, Sverdlovsk Province, Finland), *D. cherdantsevae* (Primorsky Territory), *D. calciphilus* (Primorsky Territory, Dagestan), *D. abramovae* (Tyva, Ingushetia, and Dagestan), and *D. truncatus* (Altai Republic). Descriptions, illustrations and ecological data are provided for newly described species and newly found in Russia *D. hengduanensis* and *D. daqingii*; for *D. mongolicus* an emended description, illustrations and a comparison with Chinese and Mongolian plants are given. Sporophytes are described for the first time for *Didymodon validus*; its morphological circumscription and variability are discussed.

Резюме

Данное исследование сфокусировано на проблемных группах видов в роде *Didymodon* s. str., встречающихся в России, в основном близких к *D. validus*, *D. icmadophilus* и *D. acutus*. Комбинированный морфологический и молекулярно-филогенетический подход выявил, что *D. validus* является наиболее частым видом из этой группы в России, особенно в ее азиатской части и на Кавказе, в то время как распространение *D. icmadophilus*, которое считалось очень широким, по-видимому, ограничено Кавказом, где он растет во влажных местообитаниях; нам также не удалось подтвердить принадлежность к *D. acutus* ни одного образца из России с похожим комплексом признаков. *Didymodon cordatus* спорадически встречается на юге Сибири, Дальнем Востоке и Кавказе. В азиатской части России выявлены 4 вида, которые были недавно описаны из Китая: *D. hengduanensis* в Приморском крае и Иркутской области; *D. daqingii* на юге Сибири и в Якутии; *D. tibeticus* в Забайкальском крае и *D. mongolicus* на юге Сибири, в Якутии и на Кавказе. В то же время, нам не удалось найти *D. schensianus*, который широко распространен на прилегающих территориях Китая и Японии. Шесть видов описаны как новые для науки: *D. baicalensis* (Иркутская область, Бурятия, Забайкальский край, Хакасия, Республика Алтай), *D. borealis* (Якутия, Свердловская обл., Пермский край, Финляндия), *D. cherdantsevae* (Приморский край), *D. calciphilus* (Приморский край, Дагестан), *D. abramovae* (Тыва, Ингушетия, Дагестан) и *D. truncatus* (Республика Алтай). Приводятся описания, иллюстрации и данные по экологии для новых видов и для впервые найденных в России *D. hengdianensis* и *D. daqingii*; для *D. mongolicus* дано исправленное описание, рисунок и сравнение с описанием китайских и монгольских растений. Для *Didymodon validus* впервые описаны спорофиты; обсуждаются его морфологические границы и варьирование.

KEYWORDS: mosses, new records, new species, ITS, *trn*G, molecular phylogeny

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INTRODUCTION

The genus *Didymodon*[1] is still considered to be insufficiently studied in many regions of the world. Its taxonomic revision was recently published for Europe, North Africa and Southwest and Central Asia where 30 species were recognized (Jiménez, 2006). Subsequently, Jiménez *et al*. (2022) provided a multilocus molecular-phylogenetic study of *Didymodon* s.l. and allied genera, which resulted in splitting this complex into eight genera: *Didymodon* s.str., *Geheebia*, *Gertrudiella, Husnotiella, Trichostomopsis, Tridontium, Zanderella*, and *Vinealobryum*. Their analysis included 335 samples of 89 species of *Didymodon* s.l., focusing on its intrageneric classification. Thus, each species was represented by 2–5 samples, and single-species clades in many cases were highly to maximally supported, e.g. clades of *D. rigidulus, D. acutus, D. cordatus, D. tectorum, D. hengduanensis*, etc. At the same time, clade of *D. icmadophilus* represented by samples from Europe, USA, and Venezuela appeared to be highly supported (BS 91, PP 1), and clade of *D. validus* (samples from Austria, France, Poland, and China) got lower support (BS 80, PP 0.97), indicating some heterogeneity within these species. It captured our attention because these two species are represented in herbarium collections from Russia by huge amount of so-identified samples, which are very variable and possess many questions about their identity.

The genus *Didymodon* s.str, as it is circumscribed by Jiménez *et al*. (2022) is currently represented in Russia by 11 species: *D. perobtusus, D. subandreaeoides,* and *D. nigrescens* (recently revisited by Afonina *et al*., 2022), *D. anserinocapitatus* (Otnyukova & Zander, 1998), *D. maschalogena* (Afonina *et al.*, 2010), *D. glaucus* (Ignatov & Ignatova, 3007)*, D. rigidulus, D. icmadophilus, D. acutus*, and *D. validus.* However, distribution of three latter species in its territory remains insufficiently understood. *Didymodon icmadophilus* (as *Barbula icmadophila*) was included into Russian handbooks, i.e. Abramova *et al*. (1961), Bardunov (1969) and Savicz-Lyubitskaya & Smirnova (1970), but its diagnostic characters were provided inaccurately: they correctly pointed unistratose, slightly recurved leaf margins and long excurrent costa, but described laminal cells as slightly bulging but not papillose on dorsal leaf surface (the same is written in Limpricht, 1888). Thus, many specimens from Arctic and Siberia which possessed excurrent costae and smooth laminal cells were referred to this species. *Didymodon acutus* (as *Barbula acuta*) was presented by Savicz-Lyubitskaya & Smirnova (1970) as a species rare in the USSR, occurring in its European part, Urals, Caucasus, and Middle Asia. *Didymodon validus* was treated by these authors as a variety of *Barbula rigidula*; they, however, provided its expanded description apparently based on the original description of Limpricht (1888) and mentioned that it is known in SE European part, Far East and Middle Asia. In the first checklist of mosses of the former USSR (Ignatov & Afonina, 1992) *Didymodon acutus, D. icmadophilus* and *D. rigidulus* were included, but var. *validus* was omitted. Ignatov & Ignatova (2003) provided only *D. rigidulus* for the Central European Russia, whereas *D. acutus* was addressed as not confirmed in this territory. *Didymodon validus* was also absent in regional lists of species published in the end of 20th century, e.g. of Altai Mts. (Ignatov, 1994). In the second checklist of mosses of East Europe and North Asia (Ignatov *et al*., 2006), *D. acutus* was recorded for Kaliningrad Province, South Urals and the Caucasus in Russia, *D. icmadophilus* was presented as occurring in NW European Russia and in most regions of its Asian part, whereas *D. validus* was still treated as a variety of *D. rigidulus*, and it was recorded only for Ukraine and Kyrgyzstan, but not for Russia. However, later, when an extensive bryofloristic investigation started in some regions of Asian Russia, *D. validus* became constantly present in published regional lists of mosses. *Didymodon rigidulus, D. icmadophilus* and *D. validus* were reported from Anabar Plateau (Fedosov *et al*., 2011), Suntar-Khayata Mts, Yakutia (Ivanova *et al*., 2016), Khangalassky District, Yakutia (Ivanova *et al*., 2017), Ust-Nera Region, Yakutia (Ivanova *et al*., 2018), and Zabaikalsky Territory (Afonina *et al*., 2017). In the list of mosses of Sette-Daban Mts, Yakutia (Ignatova *et al*., 2018) *D. rigidulus* was absent, but *D. icmadophilus* and *D. validus* were included; however, the latter one was marked as s.l.; similarly, *D. icmadophilus* and *D*. cf. *validus* were recorded for Ulakhan-Chistai Range, Yakutia (Ignatova *et al*., 2020).

In the course of preparation of the treatment of *Didymodon* for the ongoing volume of the Moss Flora of Russia, we faced a problem with understanding of this group of species, especially a widespread and highly heterogeneous *D. validus*, named in herbaria mainly as *D. validus* s.l. We also understood that *D. icmadophilus* was incorrectly treated in Russian handbooks, and many so-named specimens in herbaria were wrongly identified, so its distribution in Russia remained vague. The same could be said about *D. acutus*, because specimens from Russia, which more or less fitted this species in morphology, did not agree with the description of its ecology, provided, e.g., by Jiménez (2006). Furthermore, many species of *Didymodon* s. str. were recently described from China (Zhao *et al*., 2016; Jiménez *et al*., 2016, 2024; Kou *et al*., 2018, 2019, *etc*.), and presence of some of these species could be expected in neighboring territory of southern Siberia and Russian Far East. Thus we decided to apply a combined morphological and molecular-phylogenetic methods in order to clarify species identity of some problematic plants, including those identified as *D. acutus* and *D. icmadophilus*, and to understand if *D. validus* really occurs in Russia and if *D. validus* s.l. is represented by one variable species or it should be split into several taxa. This task became easier be-

[1] The authors of taxa are in accordance to Brinda & Atwood (2004), so they are omitted in the text.

cause sequences of many species were already accumulated in GenBank due to recent studies of the genus.

Material and methods

For morphological study, herbarium collections of *Didymodon* s. str. from MHA and MW were used; some duplicate specimens from LE and NSK were also studied. Traditional morphological methods were applied and some samples were selected for molecular phylogenetic study. Nuclear ITS and plastid *trn*G regions were used for checking affinities of our specimens since they show a sufficient variability for species separating in *Didymodon* and are well represented in GenBank. The laboratory protocols of DNA extraction, PCR, and sequences for ITS were essentially the same as in previous moss studies, described in detail by, e.g., Gardiner *et al.* (2005), PCR protocol for trnG followed Bakalin & Vilnet (2014). In addition to 68 specimens of *Didymodon* s. str. originally involved in molecular study (for label data and GenBank accession numbers see Appendix 1), sequences for 92 ingroup accessions were downloaded from GenBank. For GenBank accessions originally studied by Jiménez *et al.* (2022) all four molecular markers which they used (nr ITS region, plastid *trn*G intron, *trn*L–*trn*F region and atpB-rbcL spacer) were included to improve resolution of backbone phylogeny within *Didymodon* s.str. Set of outgroups for rooting the tree included 2 accessions of *Vinealobryum vinealis*, 2 of *V. eckeliae*, 1 of *Geheebia siccula*, 1 of *G. tophacea* and 1 of *G. fallax* and two accessions of *Husnotiella sinuosa*. Sequences were aligned using MAFFT v.7.520 (Katoh *et al.*, 2019) with E-INS-i strategy and otherwise default settings and then edited manually in BioEdit (Hall, 1999). Final alignment included 168 accessions and 2623 positions: 1027 of ITS and 606 of *trn*G. Indel data were scored using the simple indel coding (SIC) approach (Simmons & Ochoterena, 2000) in SeqState 1.4.1. (Müller, 2005). Bayesian analyses in MrBayes 3.2.7. (Ronquist *et al.*, 2012) were set for 10 million generations and sampling frequency one tree each 1000 generations. The chain temperature was set at 0.02 in all analyses, and GTR model with sampling throughout the model space (setting nst = mixed) was used in all analyses. Convergence of the analyses was assessed via ESS values, checked using Tracer v.1.7.2. (Rambaut *et al.*, 2018) to be higher than 200. Consensus trees were calculated after omitting the first 25% trees as burn-in. ML trees were computed in iQ-tree (Trifinopoulos *et al*., 2016) via the web server http://iqtree.cibiv. univie.ac.at/ with 1000 generations of ultrafast bootstrap default automatically assessed model of nucleotide substitutions and otherwise standard settings. Dataset was divided into three partitions, corresponding to ITS, plastid data and indels for all analyses.

Results

Obtained molecular phylogenetic trees, both inferred from Bayesian analysis and ML, are in general well resolved and supported, except few clades representing unresolved polytomies and/or not supported statistically, and, likewise, clades corresponding to individual species show high statistical support (Fig. 1). The clade that combines maximally supported clades corresponding to the genera *Vinealobryum* and *Geheebia* sensu Jiménez *et al*. (2022) is maximally supported and is situated in a sister position to the highly supported (PP1; BS97) *Didymodon* s.str. clade. Within the latter, the clade composed of Central American accessions of "*D. rigidulus* var. *subulatus*" splits first, leaving remaining accessions in several large, well supported to not supported clades, splitting one by one: (1) *D. constrictus, D. maschalogena, D. nigrescens, D. perobtusus, D. rigidulus* and *D. subandreaeoides* (PP1; BS100); (2) *D. kunlunensis* and *D. caboverdeanus* (PP1; BS100); (3) *D. acutus, D. glaucus, D. japonicas, D. jimenezii* and *D. tomaculosus* (PP1; BS99); (4) *D. daqingii, D. hengduanensis, D. icmadophilus, D. mesopapillosus, D. tibeticus* and *D. vulcanicus* (PP0.99; BS96) and ends with (5) not supported grade, crowned by not supported polytomy, which includes most of the rest of species. It represents a grade of moderately supported clades and polytomy of individual specimens and small clades. Within the later, well supported clades are mainly monospecific, corresponding to e.g. *D. anserinocapitatus, D. cordatus, D. ditrichoides, D. mongolicus, D. schensianus, D. sinicus, D. validus, D. wisselii*, or include several closely related species (e.g. *D. desertorum, D. imbricatus* and *D. tectorum*), or unite several originally involved specimens for which suitable name was not found. In addition, many clades include a supported core subclade formed by one species, and an earlier divergent "orphans", which form with the core clade a poorly supported mutual clade; also orphaned accessions appeared in the polytomy (*D. epapillatus, D. manhanensis*) and deeper in a grade (*D. obtusus*). They were retained in the tree despite of decreasing its performance and interpretability.

The newly sequenced Russian plants were found partly within clades which include known species, thus confirming close relationships of Russian plants with populations from other regions and taxonomic identity of Russian specimens. Other newly sequenced *Didymodon* samples formed supported clades without any GenBank accessions, revealing a putatively new taxa, unless the dataset is incomplete and known species are missing in it. These clades are following: (1) OK3893 found in isolated position within the supported part of backbone grade between clades 3 and 4; (2) OK3467, 3470, 4061, 4062, and 4111 (PP1; BS100), which occupies sister position to the rest of the clade 4; (3) OK3449, 3454, and 4108 (PP1; BS99) found in the not supported clade with the *D. hengduanensis* clade; (4) OK3321, 3455, 3457, 3474, 3475, 3489, 3496, 3519, and 4103 (PP1; BS100) found in the supported clade with the *D. mongolicus* clade; (5) OK3317 and 4019 (PP1; BS100) found in a sister position to *D. wisselii* clade; (6) OK3477, 4053 and 4101 (PP1; BS100) found in the not resolved polytomy within the clade 5. Their identity is dealt with in the Discussion and Taxonomy sections.

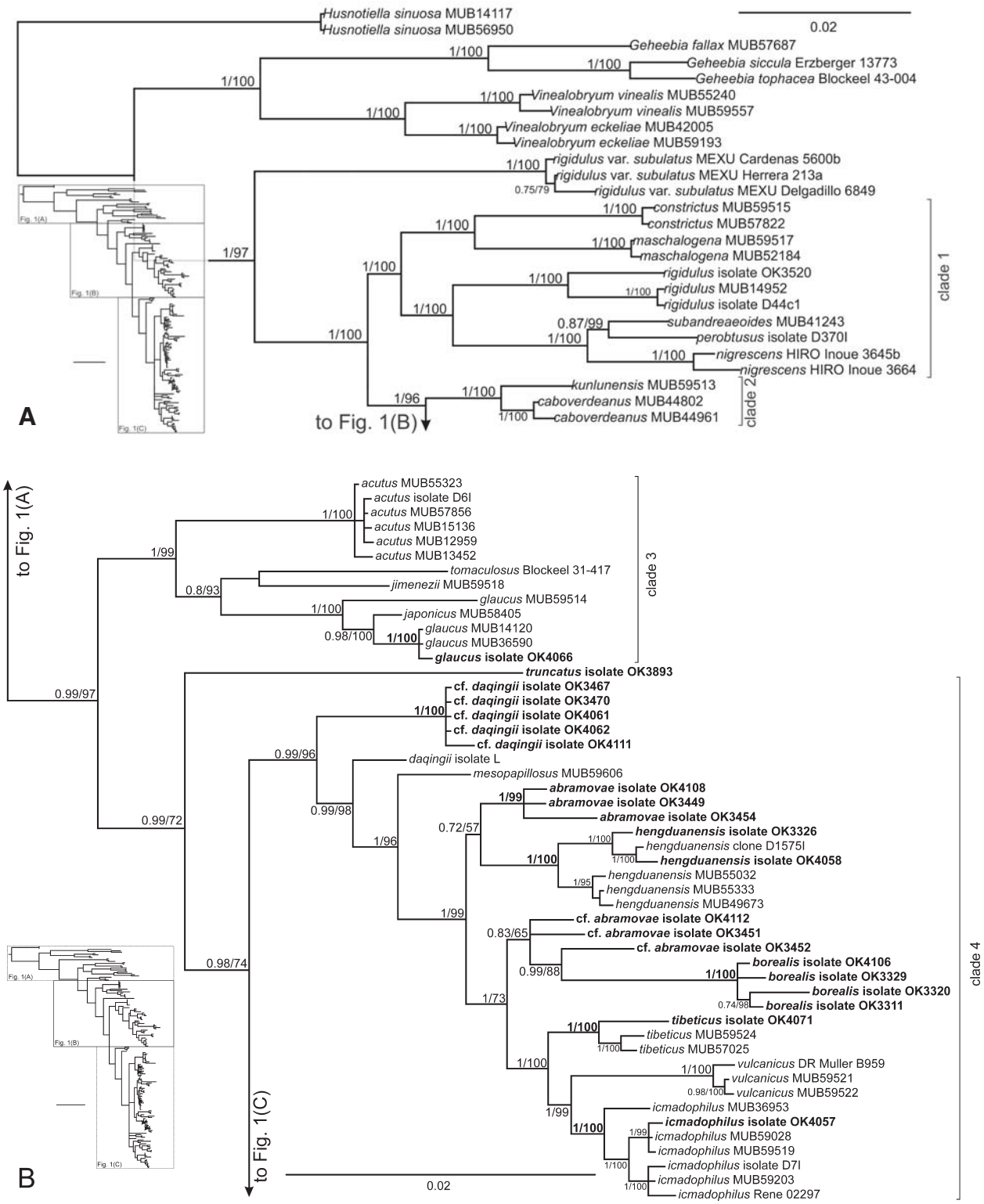

Fig. 1A, B. Bayesian phylogenetic tree of *Didymodon* s.str. inferred from the combined sequences of nr ITS region and plastid - B-*rbc*L, *trn*G & *trn*L–*trn*F. Bayesian posterior probabilities (above 0.7) inferred from the dataset with indels coded using simple indel coding approach and Bootstrap values (above 60) obtained from 1000 pseudoreplicates of ultrafast bootstrapping as implemented in iQ-tree are shown above the branches. Supports of the clades of species level, where originally studied accessions fell, are boldfaced. Major clades 1–5 distinguished within *Didymodon* s.str. (see the text) are depicted with square brackets: clades 1–2 in Fig. 1A; clades 3–4 in Fig. 1B, clade 5 in Fig. 1C.

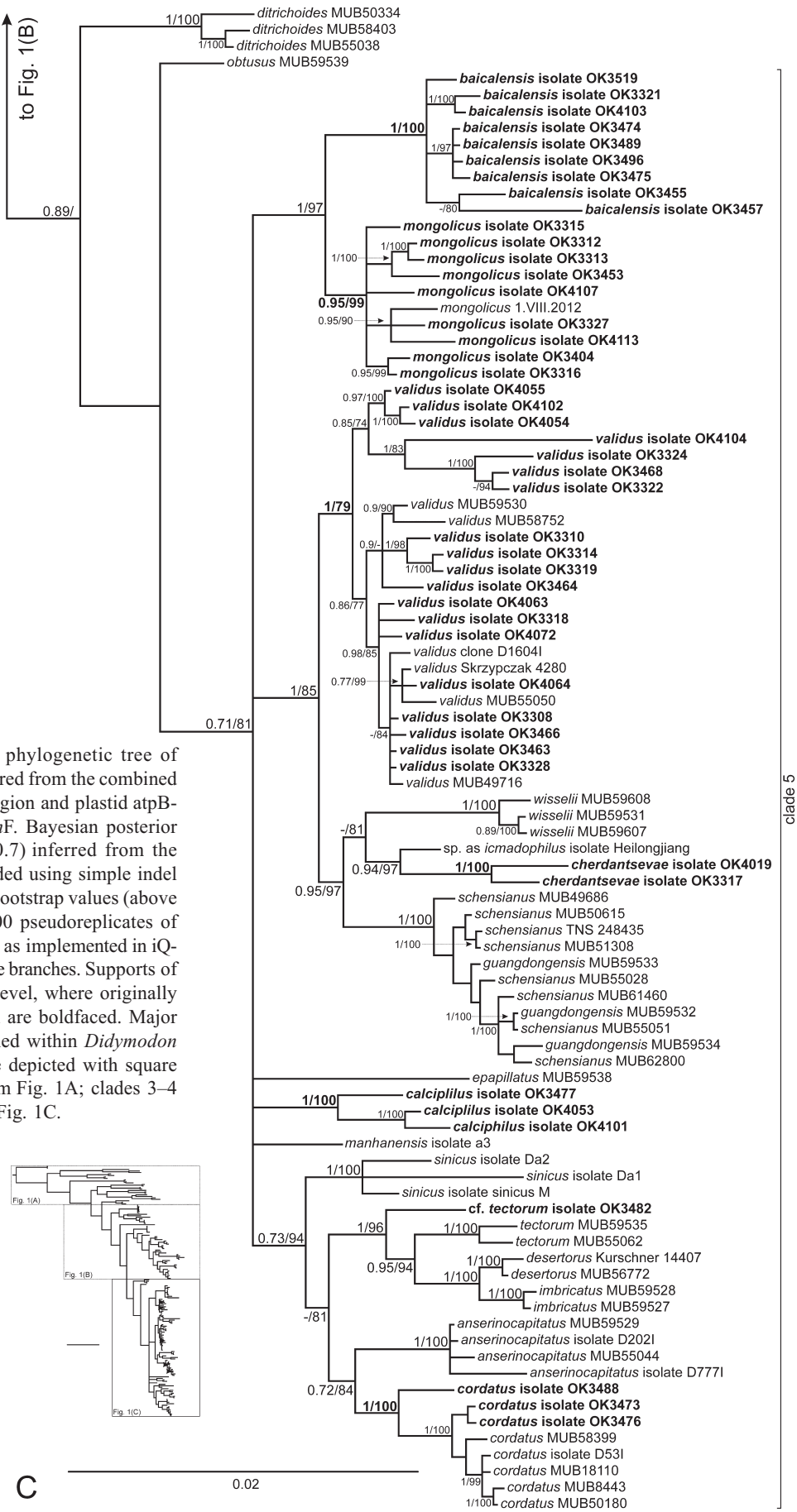

Fig. 1C. Bayesian phylogenetic tree of *Didymodon* s.str., inferred from the combined sequences of nr ITS region and plastid atpB-*rbc*L, *trn*G & *trn*L-*trn*F. Bayesian posterior probabilities (above 0.7) inferred from the dataset with indels coded using simple indel coding approach and Bootstrap values (above 60) obtained from 1000 pseudoreplicates of ultrafast bootstrapping as implemented in iQ-tree are shown above the branches. Supports of the clades of species level, where originally studied accessions fell are boldfaced. Major clades 1-5, distinguished within *Didymodon* s.str. (see the text) are depicted with square brackets: clades 1–2 im Fig. 1A; clades 3–4 in Fig. 1B, clade 5 in Fig. 1C.

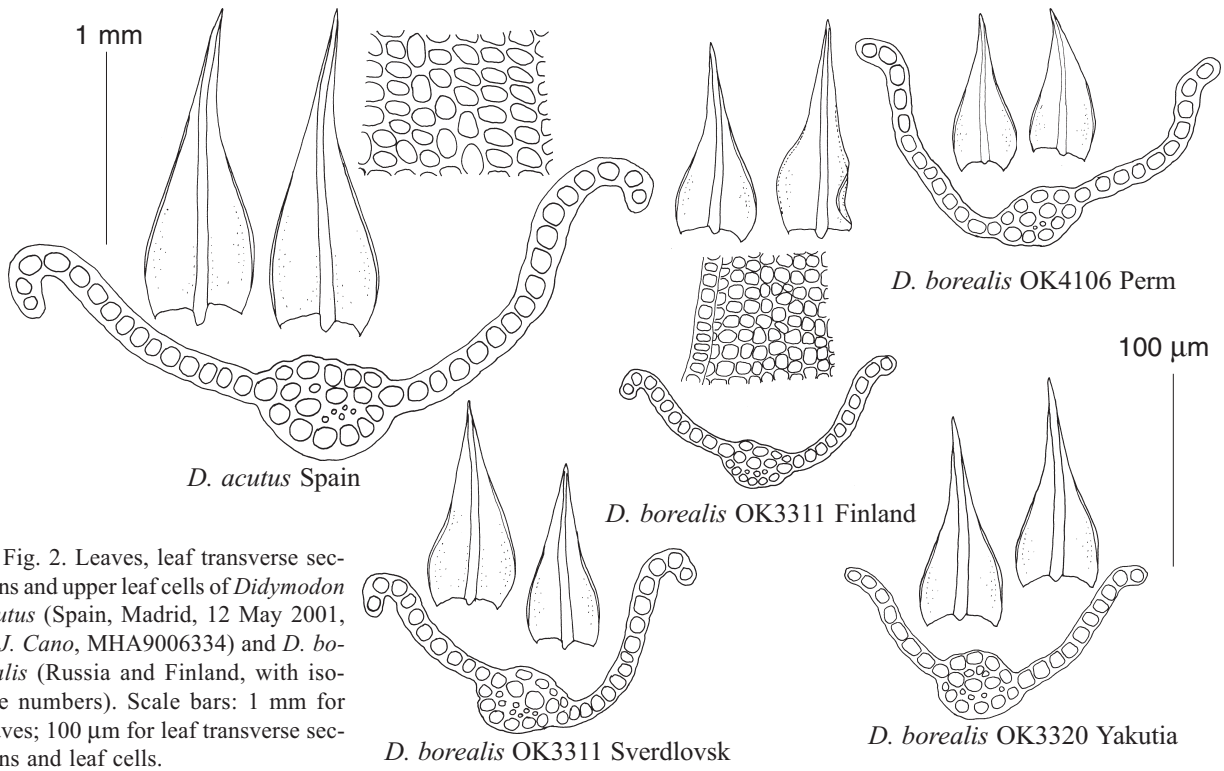

Fig. 2. Leaves, leaf transverse sections and upper leaf cells of *Didymodon acutus* (Spain, Madrid, 12 May 2001, *M.J. Cano*, MHA9006334) and *D. borealis* (Russia and Finland, with isolate numbers). Scale bars: 1 mm for leaves; 100 µm for leaf transverse sections and leaf cells.

DISCUSSION

The first clade including *D. perobtusus, D. subandreaeoides* and *D. nigrescens* will not be in the focus of the present study, it was partly discussed earlier by Afonina *et al*. (2022).

Didimodon acutus

The presence of *D. acutus* in Russia was already confirmed by Jiménez (2006), who cited one specimen of this species from North Ossetia collected by Brotherus in 1877. However, its distribution in the country remained insufficiently known, since small-sized plants with unistratose, narrowly recurved leaf margins and smooth laminal cells collected in Russia possessed a greater variability than it was provided in the description of *D. acutus*; furthermore, some of them grew in habitats which did not suite the latter species. Thus, several specimens from different regions of Russia which possessed morphological characters of *D. acutus* were sampled. Four sequences were obtained (isolates OK3311, OK3320, OK3329, and OK4106); they were resolved within the clade 4 and formed a fully supported clade with the grade of three specimens of another unknown species, contrastingly different in morphology, at its base, with low support (PP 0.83, BS 65) for their mutual clade. This clade appeared to be sister to the clade of three species, *D. tibeticus, D. vulcanius* and D. *icmadophilus*. A the same time, GenBank accessions of *D. acutus* (specimens from Greece, Italy and Spain) were found within the clade 3, in a fully supported clade sister to the clade of *D. glaucus* + *D. japonicus* + *D. jimenezii* + *D. tomaculosus*. A closer morphological comparison of specimens from Russia with the description of *D. acutus* and specimens of this species from herbaria convinced us that they likely represent another species (see Fig. 2 showing leaves, leaf transverse sections and upper laminal cells of *D. acutus* from Spain and specimens in question from Russia). We also failed to find an appropriate name for our specimens among similar species recently described from China. Considering the differences between specimens from Russia and *D. acutus* in ecological preferences, were decided to describe them as a new species, *D. borealis* (see below in Taxonomy section). However, an expanded search for *D. acutus* in herbarium collections from Russia is needed, taking into account characters of the newly described species, as well as of *D. mongolicus* (see below); molecular barcoding can be also helpful to understand better their morphological distinctions.

Didymodon icmadophilus

We selected a number of samples from Asian Russia that were identified as *D. icmadophilus* according to keys and descriptions in Russian handbooks. None of these Asian specimens were resolved together with GenBank accessions of this species. Instead, some appeared in *D. validus*-clade, while others formed a clade next to one specimen of *D. daqingii* (the species which possesses leaves with very longly excurrent costae, but have bistratose leaf margins) and in a clade sister to *D. hengduanensis*. One specimen from Irkutsk Province with leaves similar in shape to *D. icmadophilus* and weakly papillose laminal cells was resolwed in a clade with Chinese specimens of *D. hengduanensis*. However, one sample from the Caucasus collected in a moist habitat at the riv-

er bank and matching well *D. icmadophilus* in morphology was found within a fully supported *D. icmadophilus*-clade, thus confirming its presence in the Russian Caucasus. Thus, herbarium collections from Russia named as *D. icmadophilus* should be revisited to clarify its real distribution, taking into account its accurate description, e.g., by Jiménez (2006), and its ecological preferences.

Didymodon validus

This species was described from Austria (Limpricht, 1888). In Europe it is considered as vulnerable; its presence is confirmed only in France, Italy, Slovakia (Hodgetts & Lokhart, 2020) and Poland (Jiménez *et al.*, 2022). It remained neglected in Russia, probably because Savicz-Lyubitskaya & Smirnova (1970) treated it as a variety of *D. rigidulus*, and it was mainly ignored by those who identified collected specimens. This name became in use by Russian bryologists only recently, and many *Didymodon* specimens from the Caucasus and Asian Russia, having leaves with unistratose, weakly recurved margins, sharply acuminate apices, and smooth laminal cells, were identified as *D. validus*. However, in many cases this name was supplemented with "s.l." or "cf." remarks due to a considerable variability of these specimens in leaf size, leaf base differentiation, length of acumina, and leaf stature in dry and wet condition.

In the analysis by Jiménez *et al*. (2022), one specimen from China, Xinjiang appeared in a clade with European specimens of *D. validus*; it hinted on the possible wider distribution of this species in Asia, but its morphological circumscription needed to be clarified. For the present analysis, 19 specimens identified as *D.* cf. *validus* or *D. icmadophilus* were sampled; they were resolved in a moderately supported (PP 1, BS 79) clade together with all available GenBank accessions of *D. validus*. This clade appeared in a sister position to *D. wisselii* & *D. schensianus* clade. A selection of specimens in a *D. validus*-clade represents plants from a wide geographical range: Central European Russia, Caucasus, Urals, Altai Mts in southern Siberia, different regions of Yakutia, Amur Province, Khabarovsk and Primorsky Territory in the south of Russian Far East. In their main morphological characters, they do not contradict the description and illustrations of *D. validus* provided by Jiménez (2000).

Leaves and transverse sections of the sequenced specimens of *D. validus* are shown in Fig. 3. Most of these specimens have leaves with scarcely differentiated bases, without shoulders, gradually tapered into narrow acumina, having weakly recurved margins and shortly excurrent costae. Specimens from European Russia, including Urals and Caucasus, and one sample from central Yakutia have shorter (1.4–1.9 mm long) leaves than most other specimens from Asian Russia (2.2–2.9 mm long). However, all these measurements are within the range of variability of this species given by Jiménez (2000): (1.2–) 1.6–2.7(–3.2) mm. Thus, the presence and wide distribution of *D. validus* in Russia is confirmed.

Noteworthy, according to Jiménez (2006), sexual condition and sporophytes are unknown in *D. validus*. Most of our sequenced specimens were also sterile, and only in two specimens, OK3464 from Yakutia (Ust-Nera) and OK4063 from Altai (Chemal) sporophytes were found. However, we failed to find any male inflorescences in these or other specimens. Sporophytic characters of *D. validus* are described in the Taxonomy section. Jiménez (2000) also mentioned that round multicellular gemmae are often present in leaf axils in *D. validus*; in our sequenced specimens gemmae were very rare.

Didymodon cordatus

This species was already recorded in Russia from the Caucasus and Russian Far East (Ignatov *et al*., 2006). In the present study, four specimens from Russia (Dagestan Republic in the Caucasus, Altai Republic, and Primorsky Territory) were included; they were resolved within clade 5, in a maximally supported (PP 1, BS 100) subclade with four GenBank accessions of *D. cordatus* (specimens from Spain, North Ossetia/Alania, and China). Thus, species identity of Russian specimens and distribution of *D. cordatus* in the Caucasus, southern Siberia and south of the Russian Far East are confirmed.

Didymodon mongolicus

This species was described in 2016 from Northern China and Mongolia (Zhao *et al*., 2016). It was characterized as having small-sized plants, ovate leaves 0.5–1.0 mm long, with acute apices, weakly recurved margins, costa ending few cells below leaf apex, and smooth laminal cells. A singe ITS accession of *D. mongolicus* is represented in GenBank; it belongs to the holotype specimen. In our analysis it was resolved within clade 5, in a moderately supported (PP 0.95, BS 99) clade with 8 specimens from Russia (southern Siberia, Yakutia and Dagestan in the Caucasus). These specimens are partially in agreement with the description of *D. mongolicus* morphologically, including plant size, leaf shape, and unistratose, narrowly recurved leaf margins; their leaves are only slightly larger than it was provided in the original description of this species. Four specimens (from Tyva and Dagestan) also have smooth laminal cells, whereas the rest four specimens (from Yakutia, Altai and Dagestan) have laminal cells with clear, round papillae on dorsal surface (Fig. 4). In the molecular phylogenetic tree, type specimen of *D. mongolicus* forms a small, moderately supported subclade with two specimens, one of them, from Tyva being most similar to it (leaves ca. 0.8 mm long, smooth laminal cells), while another one, from Yakutia, having leaves ca. 1.1 mm long and laminal cells papillose dorsally. Jiménez (2006) states that leaf papillosity is an important morphological character for species distinguishing in *Didymodon*, but in some species leaf cells are always smooth or always papillose, but there are several species in Europe, North Africa and West Asia which may have smooth or papillose laminal cells: *D.*

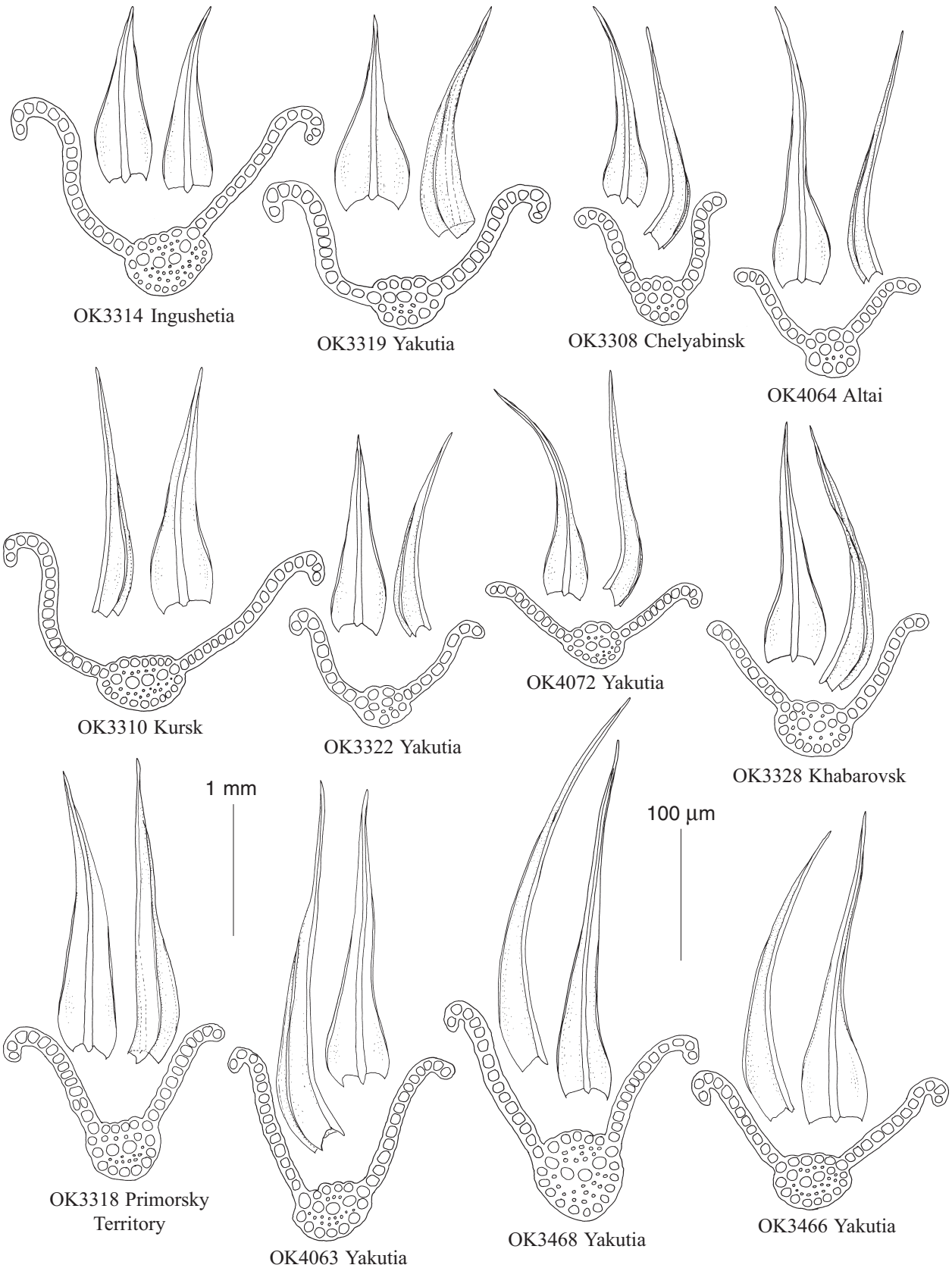

Fig. 3. Leaves and leaf transverse sections of *Didymodon validus* (from Russia, with isolate numbers). Scale bars: 1 mm for leaves; 100 µm for leaf transverse sections.

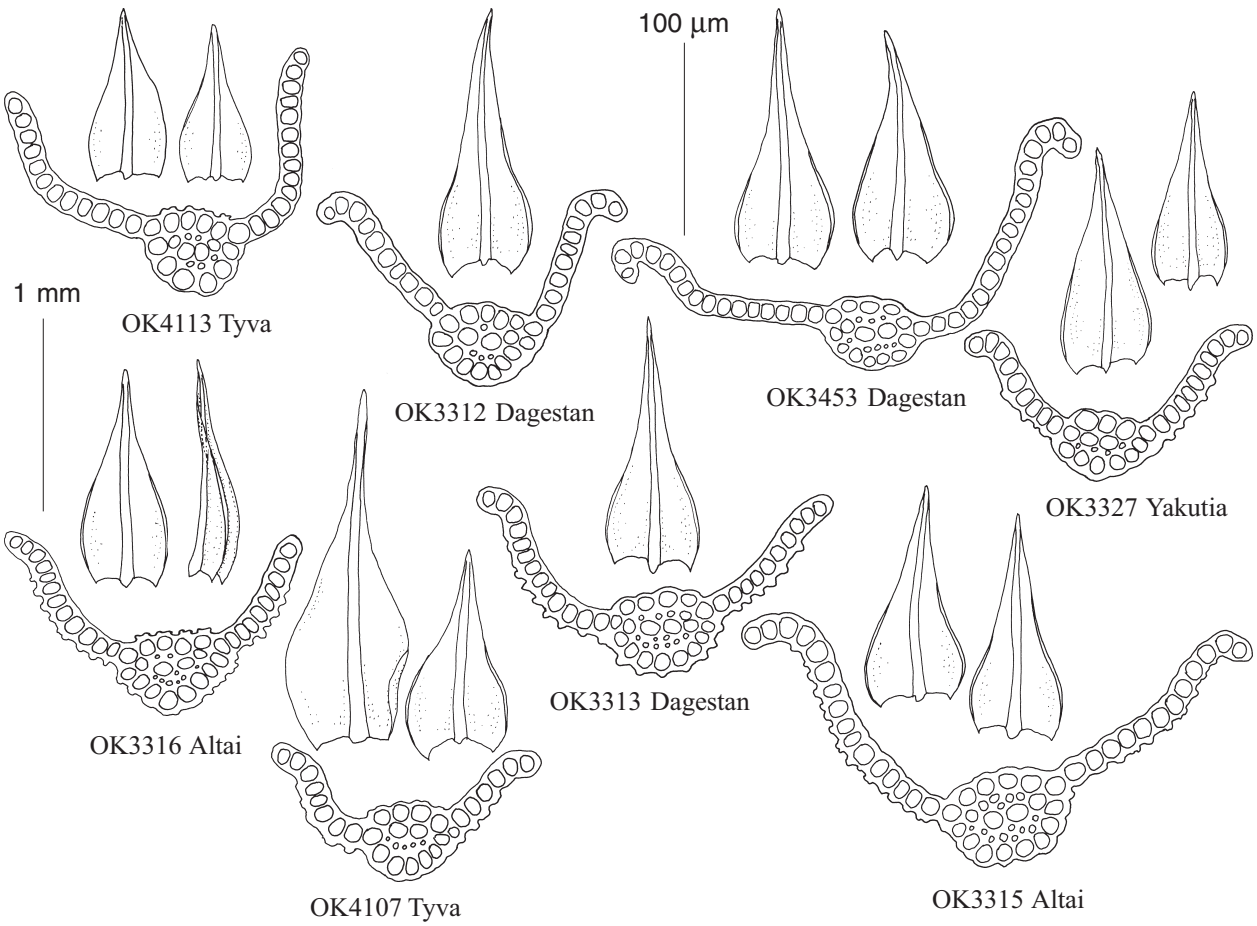

Fig. 4. Leaves and leaf transverse sections of *Didymodon mongolicus* (from Russia, with isolate numbers). For specimen 4107 from Tyva Republic (OK4107) perichaetial leaf is also shown. Scale bars: 1 mm for leaves; 100 µm for leaf transverse sections.

anserinocapitatus, D. fallax, D. maschalogena, D. subandreaeoides, and *D. tomaculosus*. It is likely that *D. mongolicus* also possesses both smooth and papillose laminal cells. At the moment, we refer all specimens from this clade to *D. mongolicus*; its expanded description is provided in the Taxonomy section.

Didymodon daqingii and ***D. manchanensis***

Didymodon daqingii was described from Inner Mongolia, China (Kou *et al*., 2019). It is a peculiar plant with a combination of morphological characters which is infrequent in *Didymodon*: bistratose upper leaf margins; costa in transverse section with 2–3 layers of guide cells and no ventral stereids; costa excurrent into a long, fragile subula; leaf bases abruptly broadened, round; and laminal cells papillose. One GenBank accession of this species obtained from the type specimen was resolved in our tree within clade 4, in the grade at the base of the clade which includes *D. icmadophilus, D. hengduanensis, D. tibeticus,* and *D. vulcanicola*. Before it in the same grade, five accessions obtained from three specimens from Asian Russia (two from Yakutia and one from Tyva) formed a maximally supported clade. These specimens possessed almost the same combination of morphological characters as *D. daqingii,* except they had smooth laminal cells. Another species with similar character combination is *D. manchanesis*; it was also described from Inner Mongolia, China (Feng *et al*., 2022). It differs from *D. daqingii* in smooth laminal cells, ovate vs. round leaf bases, and red vs. yellow-green KOH reaction. ITS obtained from the type specimen of *D. manchanensis* is also represented in GenBank. In our tree, it is resolved in an "orphaned" position within clade 5, i.e., far from *D. daqingii* and a clade of similar specimens from Russia. Our specimens, despite having smooth laminal cells, in other respects (shape of leaf base, yellow-green KOH reaction) are closer to *D. daqingii*; their ITS sequences differ from the sequence of Chinese *D. daqingii* in several substitutions, but the difference from *D. manchanensis* is greater. At the moment, we prefer to call our plants *D. daqingii*, but if other similar specimens will be found in Russia, it would be interesting to test their identity with molecular barcoding.

Didymodon tibeticus

This is another species recently described from China (Kou *et al*., 2018); it was found in several counties of Tibet Province. Three GenBank accessions of *D. tibeticus*, including obtained from paratype specimen, were available in GenBank. They formed a maximally supported clade sister to the clade of *D. icmadophilus* + *D. vulcanicus* within clade 4, and one specimen from Za-

baikalsky Territory was resolved in this clade. It also fully agreed with *D. tibeticus* in morphology and was referred to this species. The description, illustrations, ecological data and distribution in Russia are discussed separately by Afonina & Ignatova (2024) in the present volume.

Didymodon hengduanensis

This species was described in 2016 from Hengduan Mts (Yunnan, China) and was also found in Sichuan Province. Its distinctive characters include ovate-lanceolate leaves with comparatively wide bases, unistratose, recurved to revolute margins, percurrent costae, sparsely papillose laminal cells, and basal marginal cells in several rows oblate, with thickened transverse walls. Its five GenBank accessions formed a fully supported clade within clade 4, in which two specimens from Russia were resolved: one from Primorsky Territory, another from Irkutsk Province. These two specimens also fitted *D. hengduanensis* morphologically. They are described, illustrated and discussed in the Taxonomy section.

A potentially undescribed species revealed in the present analysis (see also discussion on *D. acutus* above)

(1) Two specimens from Primorsky Territory (isolates OK 3317 and OK4019) formed a maximally supported clade sister to one GenBank accession called *D. icmadophilus* from China, Heilongjiang (PP 0.94; BS 97). Their mutual clade was resolved as sister to *D. wisselii* clade without support, within clade 5. In some characters (excurrent costae, papillose leaf cells) plants from Primorsky Territory actually resembled *D. icmadophilus*, but they had leaves different in shape, widely spreading but not erect-patent when wet, and papillae on laminal cells small, sparse, present on both leaf surfaces. Their relationship to European *D. icmadophilus* was also not confirmed by molecular data, as the latter species was resolved in the clade 4 in our study, far from the specimens in question. These plants are described in the Taxonomy section under the name *D. cherdantsevae*.

(2) Four specimens (isolates OK3477, OK3484, OK4053, and OK4101) from distant localities (Primorsky Territory, Yakutia, Dagestan) formed a maximally supported clade within clade 5, without obvious relationship with other species. They were uniform morphologically and resembled *D. cordatus* in having leaves with highly recurved margins, similar costa structure, papillose laminal cells and presence of multicellular axillary gemmae; however, they had different leaf shape, with scarcely differentiated bases, and their leaf margins were only slightly recurved but not revolute. These differences together with an evidence from molecular markers suggested that this is an undescribed species; it is described in the Taxonomy section as *D. calciphilus*.

(3) Nine specimens from southern Siberia (Irkutsk Province, Buryatia, Zabaikialsky Territory, Khakassia, and Altai Republic, isolates OK3321, OK3455, OK3457, OK3474, OK3475, OK3489, OK3496, OK3519, and OK4103 formed a maximally supported clade sister to *D. mongolicus*-clade within clade 5. They are characterized by having deltoid leaves with margins revolute almost to apices, papillose laminal cells, costae in transverse section with 2–3 layers of guide cells and no ventral stereids, and multicellular axillary gemmae occasionally present. This combination of characters partially resembled *D. cordatus, D. tectorum* and *D. desertorum*, but did not exactly fit any of these species. This fact, together with data from ITS, convinced us that this is a new species. It is described in the Taxonomy section as *D. baicalensis*.

(4) Three specimens (isolates 3449, 3454 and 4108) from the Caucasus, Tyva and Yakutia were resolved within clade 4 in a highly supported (PP 1, BS 0.99) clade sister to *D. hengduanensis*, with low support for their mutual clade (PP 0.72, BS 57). These specimens are characterized by leaves tightly appressed when dry, straight, ovate-triangular, with long excurrent costae, fragile apices and unistratose laminae. This character combination is unique in *Didymodon* s. str.; thus these plants are described as a new species, *D. abramovae* in the Taxonomy section. Another three specimens with the same morphological characters (isolates OK3451, OK3452 and OK4112) from Perm Territory, Ingushetia and Tyva were found in a grade at the base of fully supported *D. borealis*-clade. We tentatively refer them to *D.* cf. *abramovae*.

(5) One morphologically very peculiar specimen from Altai Republic (isolate OK3893) was resolved in an orphaned position. Despite only one such specimen was found, it is so distinct in morphology, that we decided to describe it in order to attract attention to it and make search of similar plants easier. It is described in the Taxonomy section as *D. truncatus*.

Species that could be expected in the territory of Russia but not found in the present analysis

Didymodon schensianus

Didymodon (*Barbula*) *schensianus* was described from China, Shaanxi Province in 1896 and considered as its endemic, known from few localities. Furthermore, Li *et al*. (2001) included it into synonymy of *D. vinealis*. However, Jiménez *et al*. (2024) have shown that it is a species of its own, which has a wider distribution, being common in Japan (Honshu, Kyushu), found in Taiwan and Philippines. These authors compare *D. schensianus* with the most similar *D. hengduanensis* which was already found in Russia. However, our search in herbarium collections from the Russian Far East did not return any results, and no sequences similar to the GenBank accessions of *D. schensianus* were obtained.

Didymodon tectorum

This species was never recorded for Russia. It was described from Shaanxi Province of China; according to Li

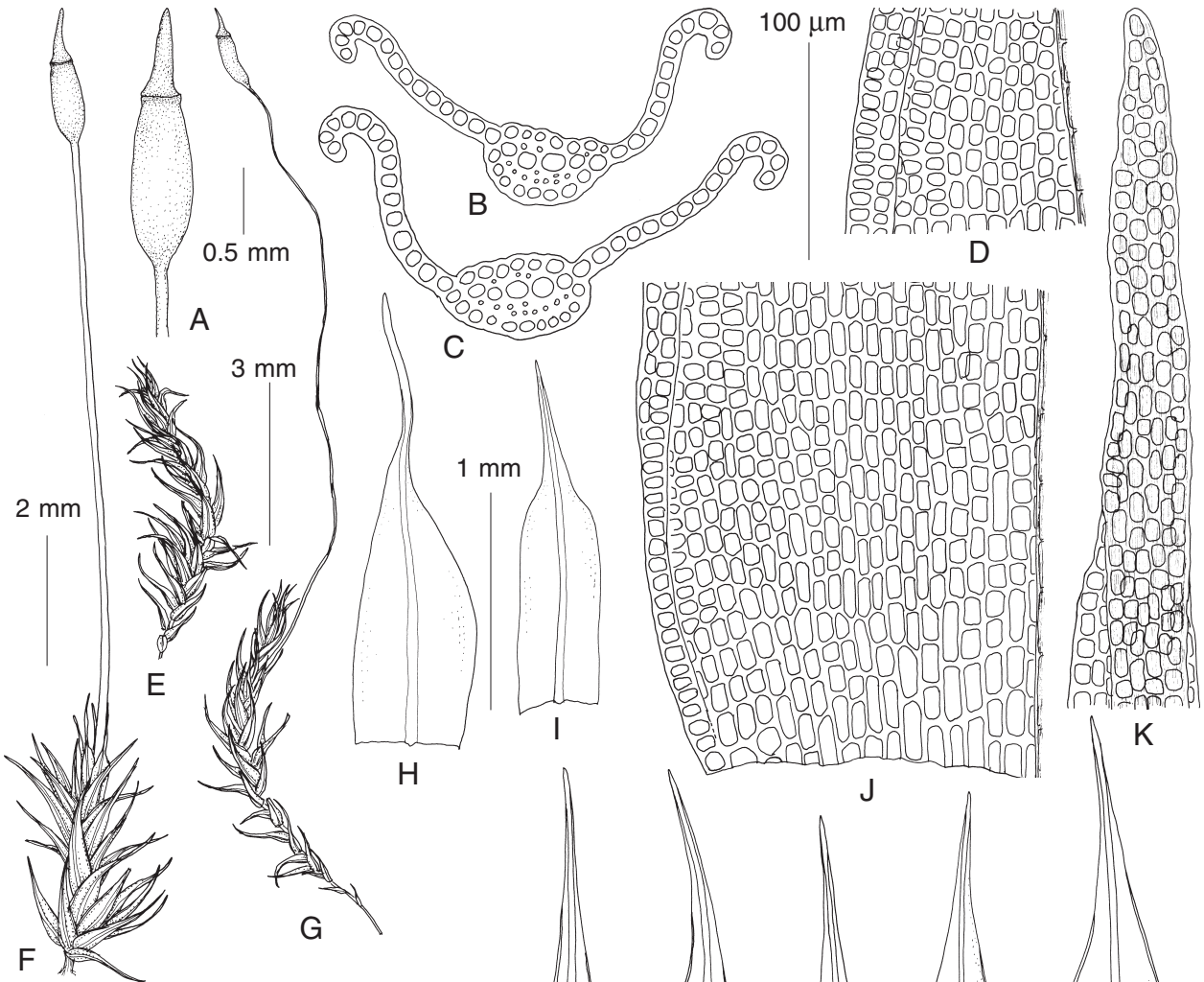

Fig. 5. *Didymodon validus* (from: Russia, Yakutia, Chersky Range, *Ignatov & Ignatova 15-1069*, MHA9101342, isolate OK3464). A: capsule; B–C: leaf transverse sections; D: mid-leaf cells; E, G: habit, dry; F: habit, wet; H–I: perichaetial leaves; J: basal leaf cells; K: upper leaf cells; L–P: leaves. Scale bars: 2 mm for E–F; 1 mm for G–I; 100 µm for A–D, J–L.

et al. (2001), it is widely distributed in China and considered to be its endemic. However, Saito (1975) reported it from Japan and Zander & Ochyra (2001) discovered it in the USA. It is very similar to *D. cordatus* morphologically: both species possess strongly revolute leaf margins almost to the apex, papillose laminal cells and multicellular axillary gemmae. In the study of Jiménez *et al*. (2022), *D. tectorum* was found to be sister to *D. imbricatus*, and their mutual clade was sister to *D. cordatus*. In our analysis, one sequence (isolate OK3482) obtained from specimen from Altai Mts had much in common with *D. tectorum* (this species was found to be most similar by BLAST search); however, it was resolved not with *D. tectorum* but in a sister position to the mutual clade of *D. tectorum* + *D. desertorum* + *D. imbricatus*. Furthermore, morphologically it did not fit any of this species but was identical to the new species described here as *D. baicalensis*; it needs additional study.

Taxonomy

Here we provide descriptions and illustrations for species newly reported from Russia (except *D. tibeticus,* which is discussed separately by Afonina & Ignatova, 2024) and described as new for science; *D. icmadophilus* is also included since its descriptions in Russian handbooks were inaccurate, and for *D. validus* the description of sporophytes is given for the first time. Other species of *Didymodon* s. str. occurring in Russia are included into the key to identification along with *D. schensianus* and *D. tectorum*, which occurrence in Russia is possible.

1. **Didymodon validus** Limpr., Laubm. Deutschl. 1: 557. 1888. Figs. 5–6.

Plants medium-sized to large, in dense or loose tufts, olive-green or brownish-green, dull. *Stems* to 3.5 cm long,

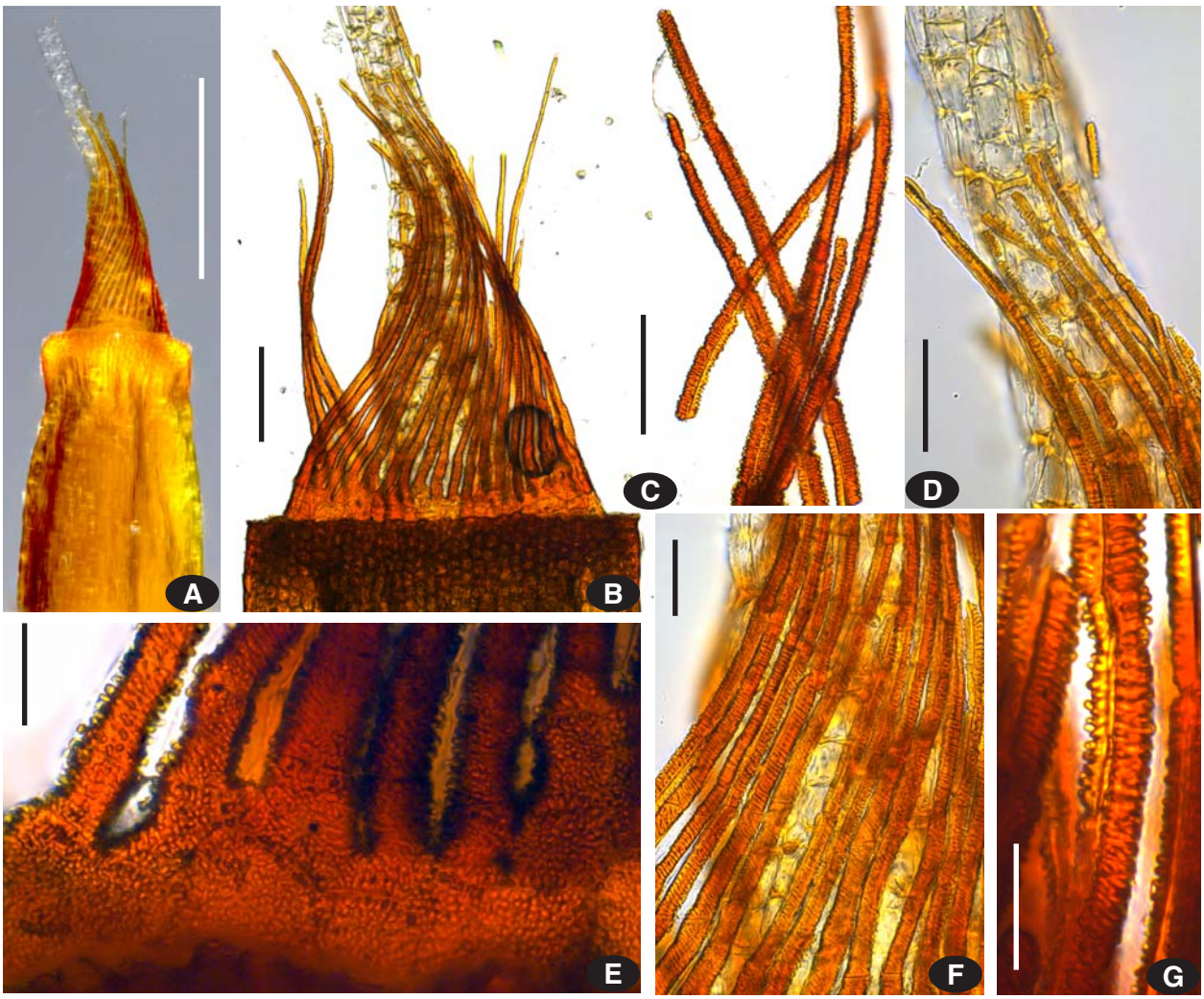

Fig. 6. *Didymodon validus* (from: Russia, Yakutia, Chersky Range, *Ignatov & Ignatova 15-1069*, MHA9101342, isolate OK3464). A–B: general view of peristome; C–D: tips of peristome teeth; E: basal membrane; F–G: close view if peristome teeth showing ornamentation of their surface. Scale bars: 0.5 cm for A; 100 µm for B; 50 µm for C–D, F; 20 µm for E, G.

erect, simple or branched, with central strand. *Rhizoidal tubers* absent. *Leaves* flexuose and incurved when dry, erectopatent to patent whan wet, ovate-lanceolate or linear-lanceolate, narrowly acute, not decurrent, (1.2–)1.6–2.8×0.6–0.8 mm, canaliculate distally; margins narrowly recurved in proximal 1/2–3/4, unistratise, entire; *costa* strong, 45–110 µm wide at leaf base, slightly narrowing upwards, excurrent into short or long mucro, prominent dorsally, flat or weakly convex ventrally, with quadrate, smooth cells on both surfaces, without band of translucent cells on ventral side below apex, in transverse section semicircular, with 4–6 guide cells in 1 layer, ventral stereids in 1–3 layers, ventral epidermis differentiated, with not bulging outer walls, dorsal stereids in 2–3 layers, dorsal epidermis present or absent; lamina unistratose; upper and median laminal *cells* rounded-quadrate, elliptic and transversely elliptic, 5–15×5–13 µm, with moderately thickened walls, smooth; basal juxtacostal cells rectangular, 12–65×5–12 µm, smooth, moderately thick-walled, chlorophyllose; basal marginal cells not differentiated or slightly shorter. KOH-reaction yellowish-green. *Asexual reproduction* by round multicellular gemmae born on branched stalks in leaf axils (rarely present in populations from Russia). Apparently *dioicous*, perigonia not seen. *Subperichaetial leaves* ca. 1.8×0.5 mm, with wide bases and subulate acumina; inner *perichaetial leaves* 1.5×0.35 mm, from rectangular bases abruptly constricted into triangilar acumina. *Setae* ca. 1.2 mm, orange-brownish. *Capsules* ovate-cylindrical, 1–1.5 mm long, brownish. *Annuli* not seen. *Opercula* conic, with long beak, ca. 0.8 mm long, cells in spiral rows. *Peristome* with low basal membrane, teeth 32, ca. 700 µm long, spirally twisted when dry, orange-brown, with oblique ridges and dense, spiculose papillae. *Spores* 11–16 µm. *Calyptrae* not seen.

Didymodon validus is widespread in the Caucasus and southern regions of Asian Russia. It differs from other species with unistratose leaf laminae, including margins, and smooth laminal cells, in having larger leaves and acumina longer than bases (from *D. mongolicus, D. borealis* and *D. acutus*) or in shorter excurrent costa and not fragile leaf tips (from described here

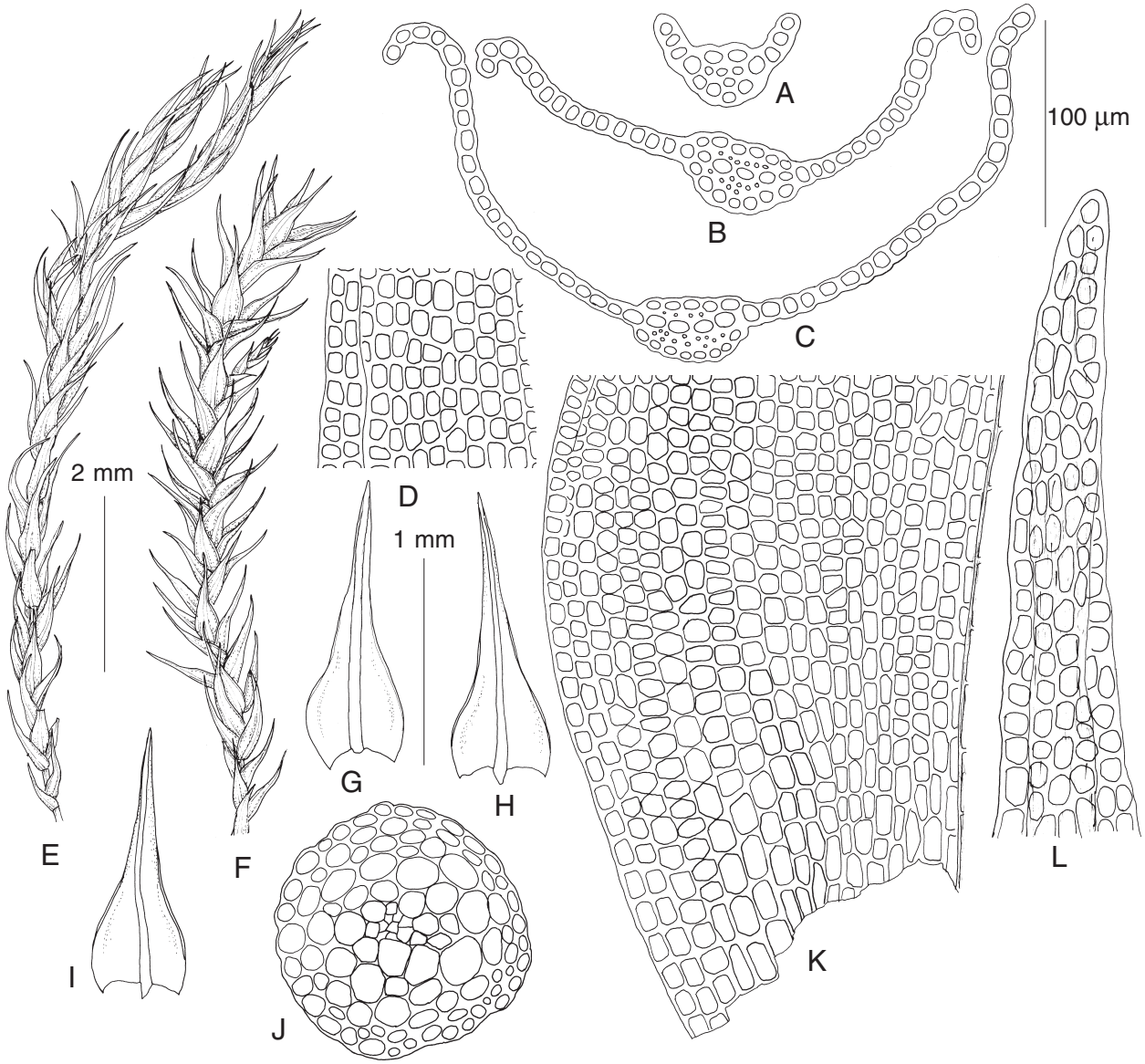

Fig. 7. *Didymodon borealis* (from holotype). A–C: leaf transverse sections; D: mid-leaf cells; E: habit, dry; F: habit, wet; G–I: leaves; J: stem transverse section; K: basal leaf cells; L: upper leaf cells. Scale bars: 2 mm for E–F; 1 mm for G–I; 100 µm for A–D, J–L.

D. abramovae).

2. **Didymodon borealis** Ignatova & Ignatov, species nova. Fig. 7.

Didymodon borealis differs from otherwise similar *Didymodon acutus* in smaller size of plants, leaves 0.7–0.85×0.25–0.3 mm versus 0.8–1.8×0.3–0.65 mm, and thinner-walled leaf cells.

Type: Russia, Yakutia, Tomponsky District, small Creek – left tributary of Dyby River, 62°44’51”N, 139°04’46”E, 765 m a.s.l., on verticall cliff wall on right bank of the creek, 27.VIII.2017, *Ignatov & Ignatova 17-426* (holotype MHA9025679, isotype MW9092501).

Etymology: species name reflects a peculiarity of its distribution area, as all its currently known localities are within boreal areas of Eurasia.

Plants tiny, in dense, often easily separating tufts, dull brownish-green or olivaceous-green. *Stems* to 1 cm long, erect, simple or branched, without hyalodermis, with central strand. *Rhizoidal tubers* absent. *Leaves* straight, appressed when dry, erectopatent when wet, ovate-lanceolate, from ovate bases abruptly or gradually narrowed into triangular acumina as lonf as the bases or slighly longer, narrowly acute or acuminate, not decurrent, 0.6–0.85×0.25–0.30 mm, canaliculate distally; margins narrovly recurved at proximal 1/2–2/3, unistratose, entire; *costa* 50–60 µm wide at base, slightly narrowing upwards, percurrent, moderately prominent distally, slightly convex ventrally, with quadrate, smooth cells on both surfaces, without band of translucent cells on ventral side below apex, in transverse secrion elliptic, weakly differentiated in the uppermost portion, below with 3–5 guide cells in 1 layer, ventral stereids in 0–1 layer, ventral epi-

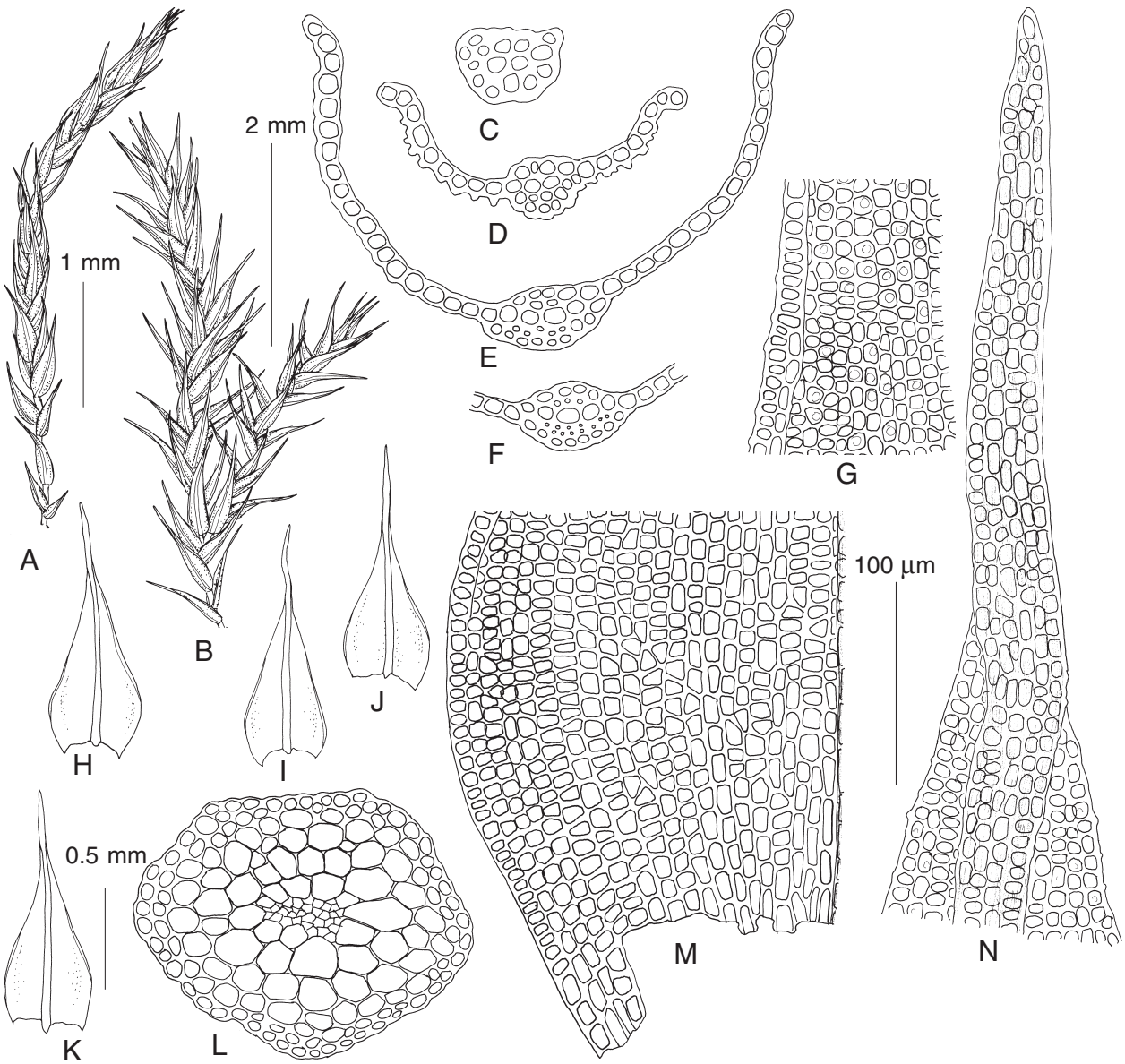

Fig. 8. *Didymodon icmadophilus* (from Russia, Caucasus, Karachaevo-Cherkessian Republic, Teberdinsky Nature Park, *Ignatov & Ignatova 05-3531*, MW9035941, isolate OK4057). A: habit, dry; B: habit, wet; C–F: leaf transverse sections; G: mid-leaf cells; H–K: leaves; L: stem transverse section; M: basal leaf cells; N: upper leaf cells. Scale bars: 2 mm for B; 1 mm for A; 0.5 mm for H–K; 100 µm for C–G, L–N.

dermis differentiated, with outer walls not bulging, dorsal stereids in 1–2 layers, dorsal epidermis present or absent; lamina unistratose; upper and median laminal *cells* rounded-quadrate, elliptic and transversely elliptic, 6–14×9–12 µm, with moderately thickened walls, smooth; basal cells weakly differentiated, basal juxtacostal cells short rectangular and quadrate, 12–20×11–12 µm, smooth, with moderately thickened walls, chlorophyllose; basal marginal cells in several rows short rectangular, quadrate and travsversely elliptic. KOH-reaction yellowish-green. *Specialized asexual reproduction* absent. Apparently *dioicous*, only male plants seen. *Perigonia* terminal. *Perichaetia* and *sporophytes* unknown.

Didymodon borealis is currently known from Yakutia, Urals (Perm Territory and Sverdlovsk Province) and SW Finland. It grows on wet, rarer moderately dry cliff walls in the forest, along streams and rivers. It can be confused with *D. acutus* and forms of *D. mongolicus* with smooth cells; however, both these species have larger leaves (see key) and grow in xeric habitats.

3. **Didymodon icmadophilus** (Schimp. ex Müll. Hal.) K. Saito, J. Hattori Bot. Lab. 39: 519. 1975. — *Barbula icmadophila* Schimp. ex Müll. Hal., Syn. Musc. Frond. 1: 614. 1849. Fig. 8.

Plants small to medium-sized, in dense tufts, brownish-green, olivacous-green or brownish, dull. *Stems* to 3.5 cm long, erect, simple or branched, with central strand. *Rhizoidal tubers* absent. *Leaves* erect, appressed when dry, erect-patent to spreading when wet, ovate-lanceolate, lan-

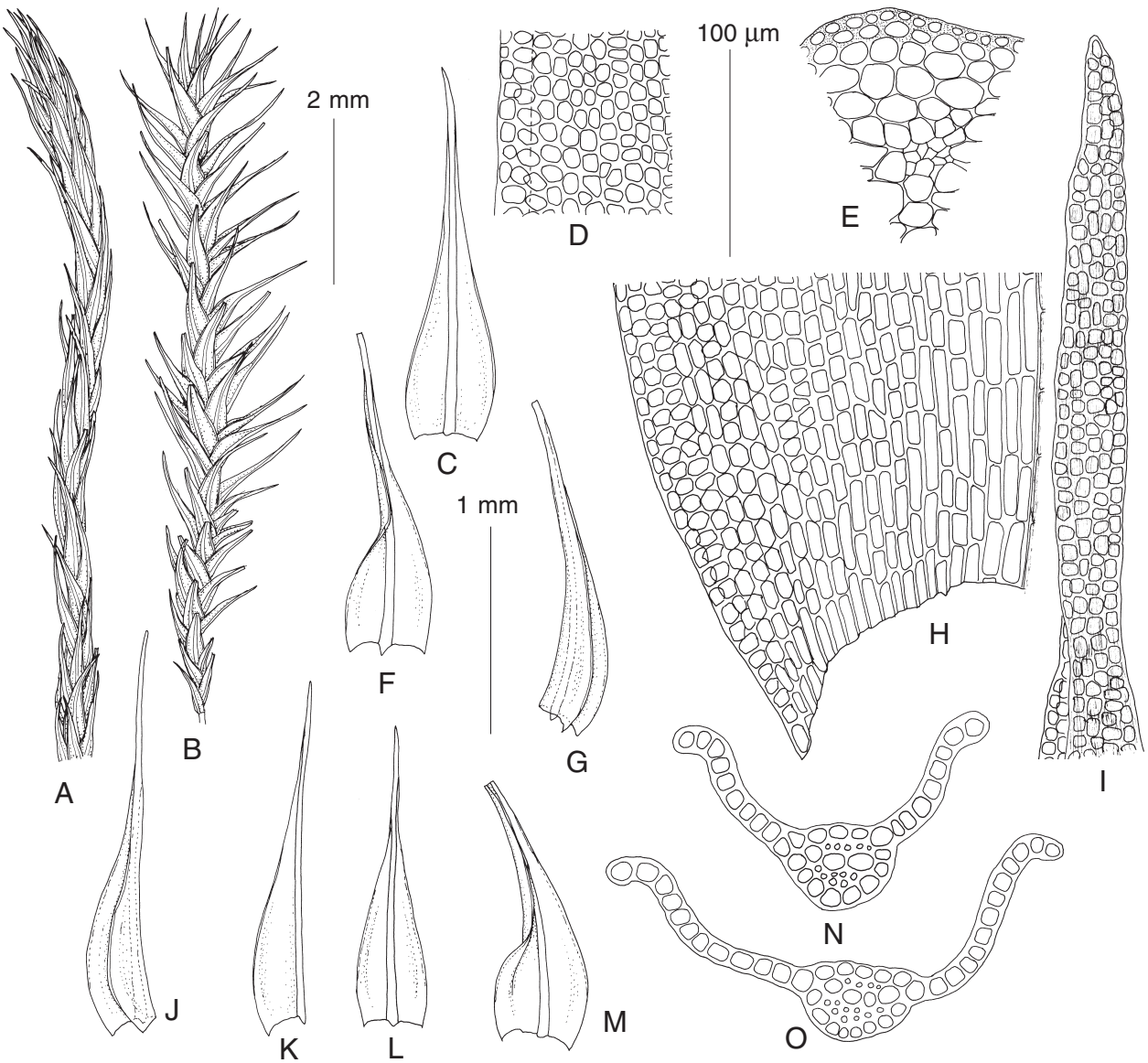

Fig. 9. *Didymodon abramovae* (from holotype). A: habit, dry; B: habit, wet; C, F–G, J–M: leaves; D: mid-leaf cells; E: stem transverse section; H: basal leaf cells; I: upper leaf cells; N–O: leaf transverse sections. Scale bars: 2 mm for A–B; 1 mm for C, F–G, J–M; 100 µm for D–E, H–I, N–O.

ceolate or ovate-triangular, acuminate, not decurrent, 0.6–2.2×0.3–0.6 mm, canaliculate distally; margins narrowly recurved in proximal 1/2, unistratose, entire; *costa* moderately strong, 30–85 µm wide at base, weakly narrowing upwards, excurrent into long subula to 0.25 of leaf length, weakly prominent dorsally, on ventral side flat or weakly convex, on both surfaces with quadrate cells, smooth on ventral surface, smooth or papillose on dorsal surface, without band of translucent cells on ventral side below apex, in transverse section semicircular, with 3–5 guide cells in 1 layer, ventral stereids in (0)1–2 layers, ventral epidermis differentiated, with outer walls not bulging, dorsal stereids in 2–3 layers, dorsal epidermis differentiated; lamina unistratose; upper and median laminal *cells* rounded-quadrate, elliptic and transversely elliptic, 5–13×5–13 µm, with moderately thickened walls, papillose, with papillae mainly on dorsal surface, occasionally also with few papillae on ventral surface, simple or bifurcate, occasionally low; basal juxtacostal cells rectangular and quadrate, 8–40×5–13 µm, smooth, with moderately thickened walls, chlorophyllose; basal marginal cells not differentiated or slightly shorter. KOH-reaction yellowish or orange. *Specialized asexual reproduction* absent. *Dioicous*, *sporophytes* rare, in the territory of Russia unknown.

This species was recorded from many areas in Russia, but most these records were erroneous, based on specimens actually belonging to other species, mainly *D. validus*, sometimes *D. daqingii* or described here *D. abramovae*. Here we confirm the identity of one specimen of *D. icmadophilus* from the Caucasus, Karachevo-Cherkessian Republic, Teberdinsky Nature Park, where it was collected on wet rocky soil near waterfall. Leaves with

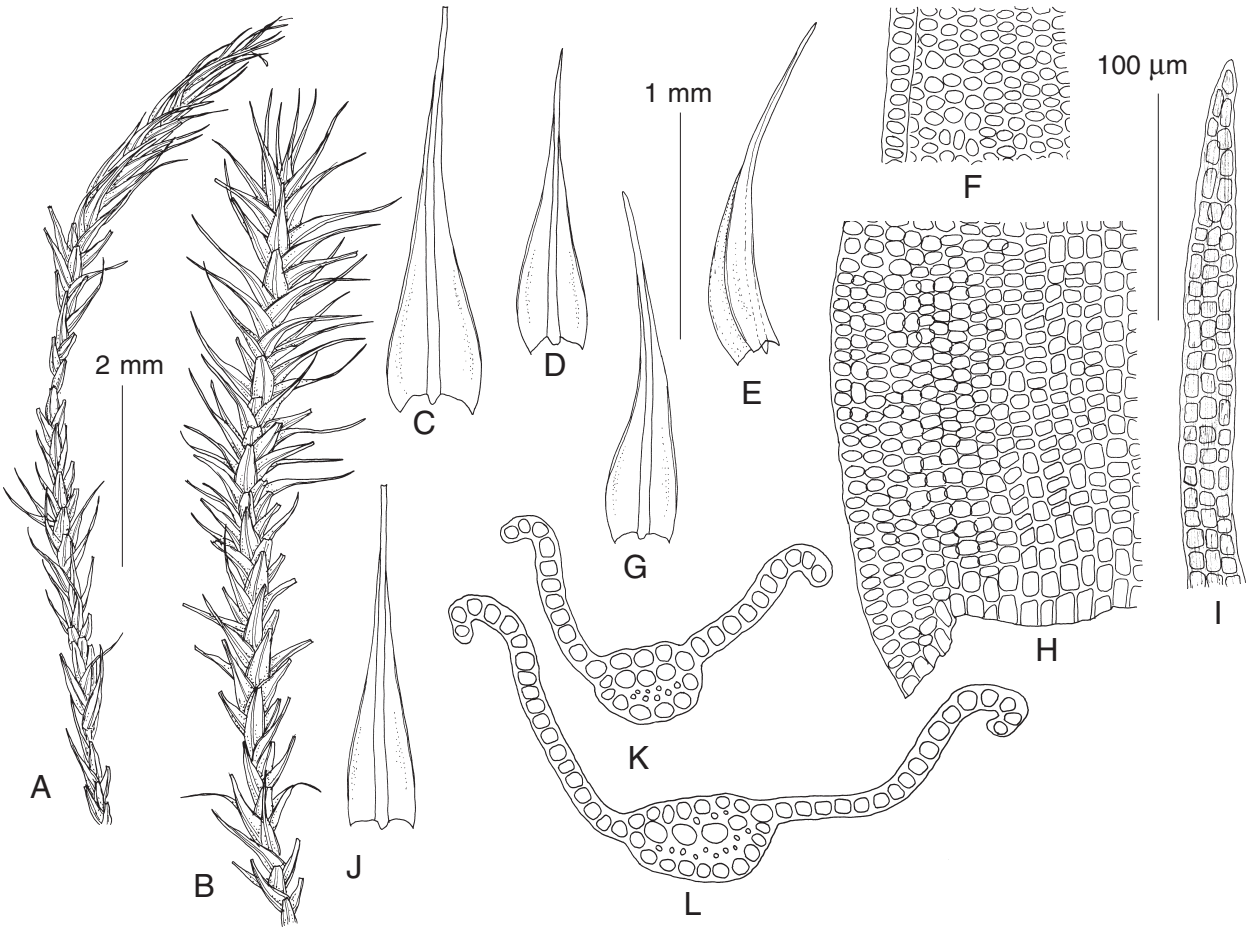

Fig. 10. *Didymodon* cf. *abramovae* (from Russia, Republic of Tyva, Kara-Khol Lake, *Pisarenko 23/3*, NSK, MHA9131862, isolate OK4112). A: habit, dry; B: habit, wet; C–E, G, J: leaves; F: mid-leaf cells; H: basal leaf cells; I: upper leaf cells; K–L: leaf transverse sections. Scale bars: 2 mm for A–B; 1 mm for C–E, G, J; 100 µm for F, H–I, K–L.

long-excurrent costae are also characteristic for *D. daqingii* and described here *D. abramovae*. First of these species can be separated by bistratose leaf margins and costae with two layers of guide cells and no ventral stereids; leaves of *D. abramovae* are more gradually tapered from ovate base and possess smooth laminal cells.

4. **Didymodon abramovae** Ignatova & Fedosov, species nova. Figs. 9–10.

Type: Russia, Caucasus, Republic of Dagestan, Gunib District, 42°25'N, 46°54'E, 1850 m alt., near research station of Mountain Botanical Garden, northern macroslope of Mayak Mt., exposed N-faced rock outcrops, 20.V.2009, *Ignatov & Ignatova 09-607* (Holotype MHA9101354, isotype MW9035943).

Etymology. The species in named in honor of Anastasia Lavrentievna Abramova (1915–2012), russian bryologist, who greatly contributed to the knowledge on moss flora of Russia, in particular of the Caucasus and Russian Arctic.

Plants medium-sized, in loose or dense tufts, green, yellowish-green or brownish, dull. *Stems* 1–1.5 cm long, simple or branched, without hyalodermis, with central strand. *Rhizoidal tubers* absent. *Leaves* erect, appressed when dry, patent to spreading when wet, ovate-triangular, with scarcely differentiated bases, gradually narrowed into subulate acumina, with fragile apices, 1.5–2.1×0.35–0.5 mm, canaliculate distally; margins narrowly recurved in proximal 1/3–3/4, unistratose, entire; costa 45–60 µm wide at leaf base, slightly narrowing upwards, excurrent into long chlorophyllose awn, prominent dorsally, flat distally, on both surfaces with quadrate cells, smooth, without band of translucent cells on ventral side below apex, in transverse section semicircular, with 3–6 guide cells in 1 layer, ventral stereids in 0(1) layer, ventral epidermis differentiated, with not bulging outer walls, dorsal stereids in 1–2 layers, dorsal epidermis differentiated; lamina unistratose; upper and median laminal *cells* rounded-quadrate, irregularly polygonal, elliptic and transversely elliptic, 6–13×4–11 µm, with moderately thickened walls, collenchymatose, smooth; basal juxtacostal cells rectangular, 20–40×7–11(–13) µm, or short rectangular to quadrate, 7–18×9–11 µm, smooth, with moderately thickened, straight walls; basal marginal cells in several rows oblate, collenchymatose. KOH-reaction yellowish-green. *Specialized asexual reproduction* absent. *Gametangia* and *sporophytes* unknown.

Didymodon abramovae is currently known from the Caucasus, Tyva and Yakutia. We also tentatively refer to

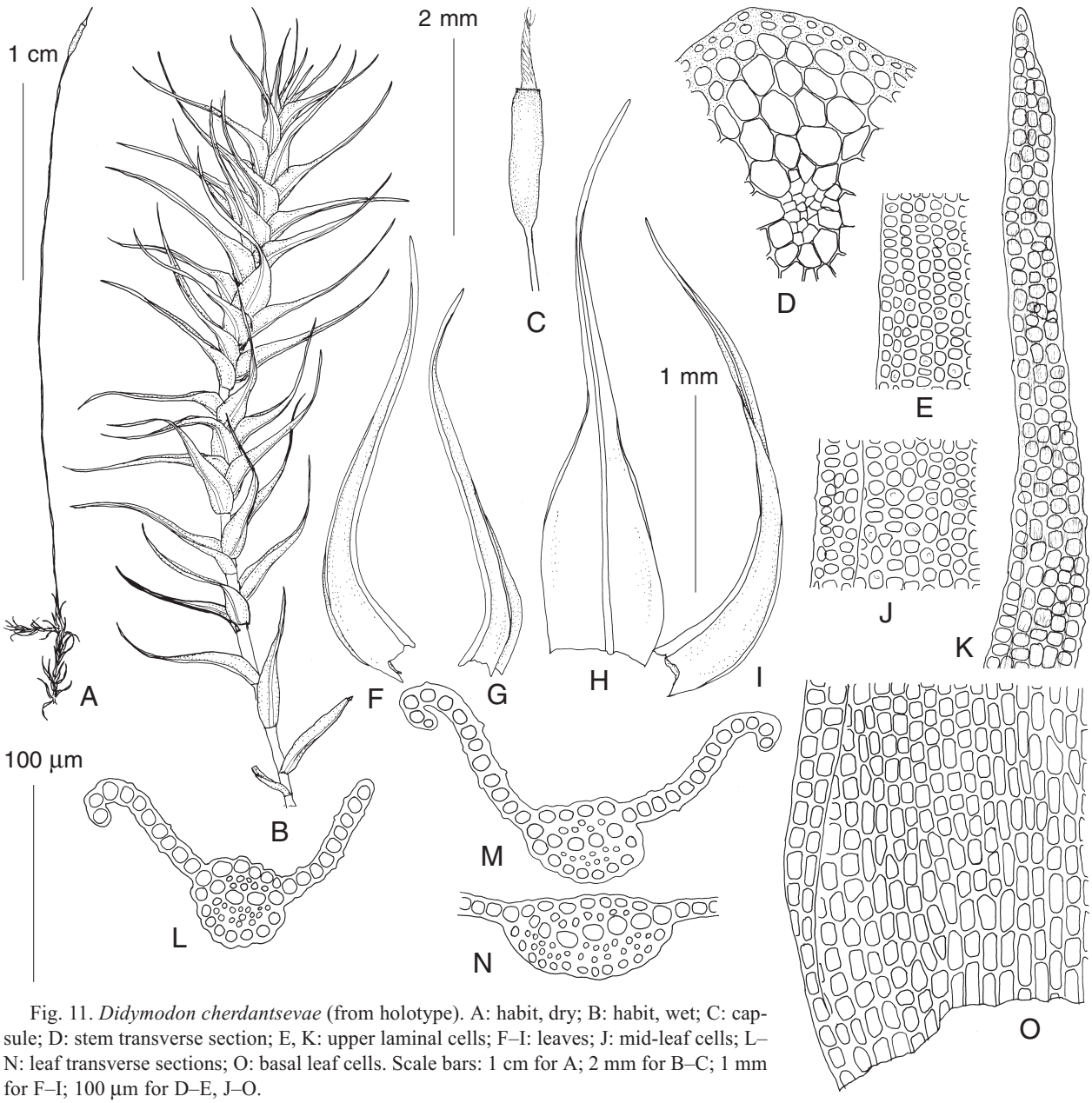

Fig. 11. *Didymodon cherdantsevae* (from holotype). A: habit, dry; B: habit, wet; C: capsule; D: stem transverse section; E, K: upper laminal cells; F–I: leaves; J: mid-leaf cells; L–N: leaf transverse sections; O: basal leaf cells. Scale bars: 1 cm for A; 2 mm for B–C; 1 mm for F–I; 100 µm for D–E, J–O.

it three other specimens, including one from Perm Territory. Its leaves with long excurrent costa make it similar to *D. icmadophilus*, but the latter species has leaves with wider bases, abruptly narrowed into acumina, and laminal cells papillose on dorsal surface. Long excurrent costa and fragile leaf apices are also characteristic for *D. daqingii*, but it can be distinguished from *D. abramovae* by bistratose leaf margins and costa with 2–3 layers of guide cells and no ventral stereids. *Didymodon validus* differs from *D. abramovae* by shorter excurrent costae, not fragile leaf apices, and leaves flexuose and incurved when dry (straight and appressed in *D. abramovae*).

5. **Didymodon cherdantsevae** Ignatova & Fedosov, species nova. Fig. 11.

Type: Asian Russia, Primorsky Territory, Russky Island, vicinity of Melkovodnaya Bay, gentle forested slope of Russkaya Creek valley, 43.0021°N, 131.80941°E, 23 m alt., oak dominated forest with rock outcrops, roadside, 14.IX.2024 *Fedosov 24-351* (Holotype MW9092502, isotype MHA).

Etymology. The species in named in honor of Valentina Yakovlevna Cherdantseva (1939–2013), russian bryologist, who greatly contributed to the knowledge of moss flora of the southern Russian Far East.

Plants medium-sized, in loose tufts, green or yellowish-green, dull. *Stems* ca. 1 cm long, simple or branched, without hyalodermis, with central strand. *Rhizoidal tubers* absent. *Leaves* slightly flexuose and incurved when dry, widely spreading when wet, forming an angle ca. 90° with stem, occasionally with reflexed apices, S-shaped in side view, from short rectangular bases gradually narrowed into long, narrow triangular acumina, exceeding bases 1.5–2 times in length, acuminate, not decurrent,

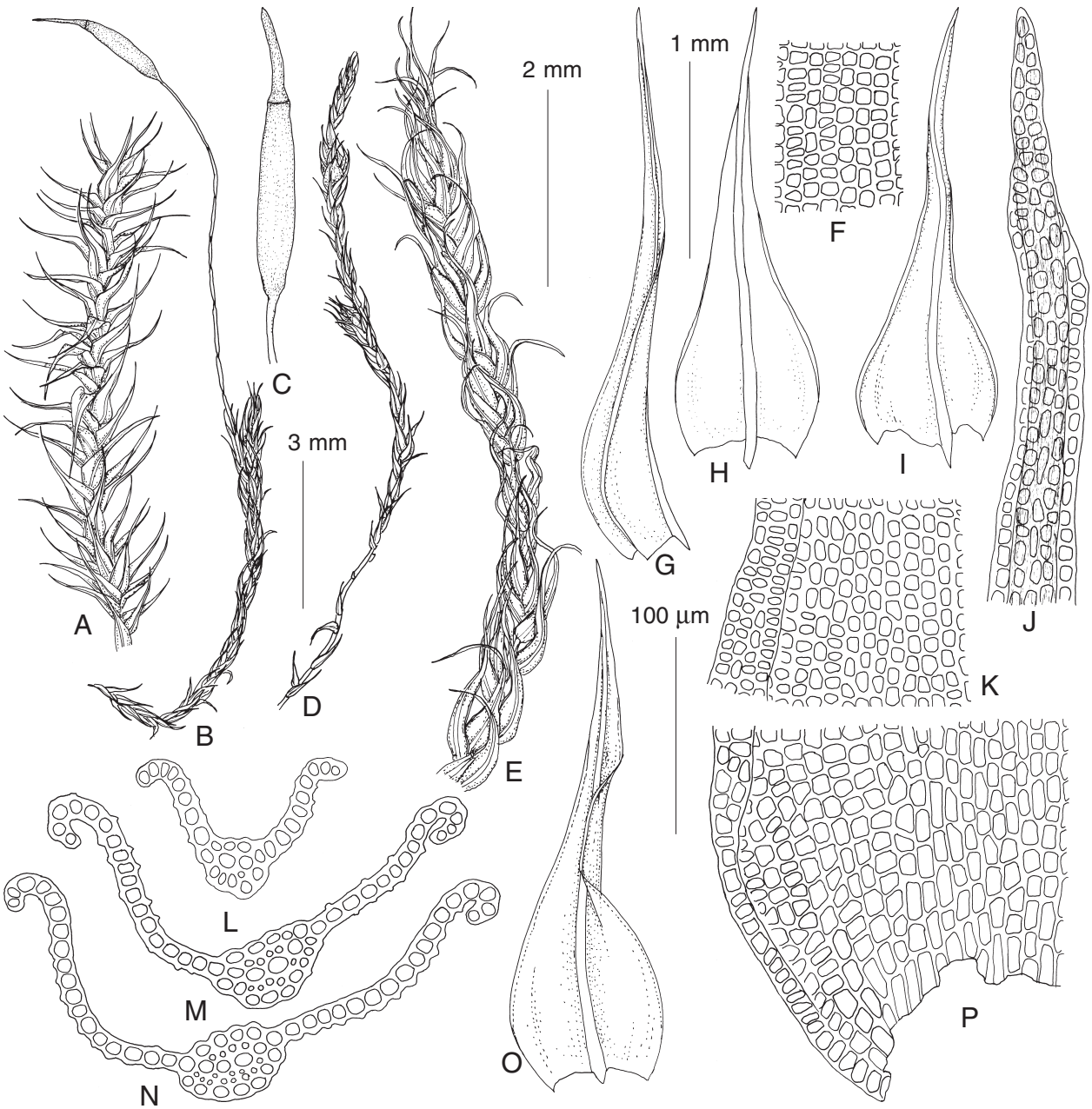

Fig. 12. *Didymodon hengduanensis* (A, F–P from: Russia, Primorsky Territory, Sedaya Mt., *Ignatov & Ignatova 13-1517*, MHA9109153; isolate OK3326; B–D from: Russia, Irkutsk Province, Slyudyanka, *Ignatov et al. 18-4492*, MW9090873, isolate OK4058). A: habit, wet; B: plant with sporophyte; C: capsule; D: male plant; E: habit, dry; F, J: upper laminal cells; G–I, O: leaves; K: mid-leaf cells; L–N: leaf transverse sections; P: basal leaf cells. Scale bars: 3 mm for A–B, D; 2 mm for C, E; 1 mm for G–I, O; 100 µm for F, J–N, P.

1.7–1.9×0.3–0.35 mm, canaliculate distally; margins narrowly recurved in proximal 1/3–3/4, unistratose, entire; costa 40–50 µm wide at leaf base, slightly narrowing upwards, excurrent into short mucro, prominent dorsally, flat ventrally, on both surfaces with quadrate cells, smooth, without band of translucent cells on ventral side below apex, in transverse section semicircular, with 3–6 guide cells in 1 layer, ventral stereids in 1(2) layers, ventral epidermis differentiated, with weakly bulging outer walls, dorsal stereids in 2–4 layers, dorsal epidermis differentiated; lamina unistratose; upper and median laminal *cells* rounded-quadrate, elliptic and transversely elliptic, 8–11×8–10 µm, with moderately thickened walls, weakly papillose on both surfaces; basal juxtacostal cells short rectangular, 13–25×7–9 µm, smooth, with moderately thickened, straight walls; basal marginal cells in several rows shorter, short rectangular and quadrate. KOH-reaction yellow. *Specialized asexual reproduction* absent. *Dioicous*. *Perigonia* lateral. *Setae* ca. 2 cm long, reddish-brown. *Capsules* cylindrical, 1.5 mm long, straight, light brown. *Annuli* not seen. *Opercula* high conic, straight, ca. 1 mm long. *Peristome* with very low basal membrane, teeth 32, 750–770 µm long, spirally twisted when dry, densely papillose. *Spores* 9–11 µm.

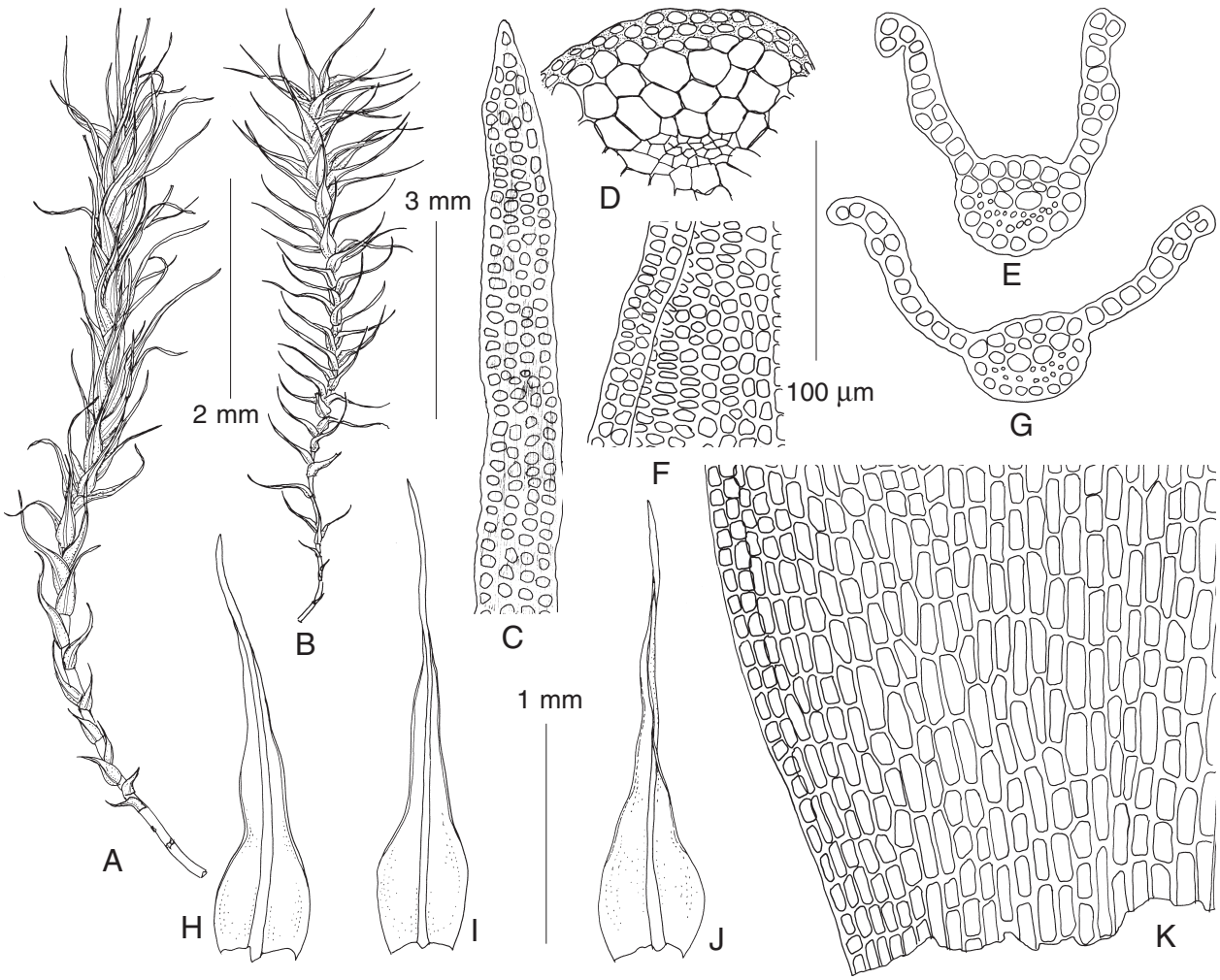

Fig. 13. *Didymodon daqingii* (from: Russia, Yakutia, Suntar Khayata Range, *Ignatov & Ignatova 15-11*, MHA9108739; isolate OK4062). A: habit, dry; B: habit, wet; C: upper laminal cells; D: stem transverse section; E, G: leaf transverse sections; F: mid-leaf cells; H–J: leaves; K: basal leaf cells. Scale bars: 3 mm for B; 2 mm for A; 1 mm for H–J; 100 µm for C–G, K.

Calyptrae not seen.

Didymodon cherdantsevae is currently known only from Primorsky Territory, on Russky Island and in Dalnegorsk District, near Sedaya Mt. In both localities it was collected at roadsides, on a rubble scree and rocky soil. Another species having leaves with comparatively short bases, long acumina, and weakly papillose laminal cells is *D. hengduanensis*; it was described from China and revealed in Russia in the present study. It differs from *D. cherdantsevae* by sligtly larger leaves with wider bases, 1.8–2.7×0.6–0.9 mm vs 1.7–1.9×0.3–0.35 mm, erecto-patent to patent when moist (spreading at 90° with stem in *D. cherdantsevae*), and less strong stereid bands in transverse sections of costa.

6. **Didymodon hengduanensis** J.A. Jiménez, D.G. Long, Shevock & J. Guerra, Phytotaxa 275(3): 288, 1, 2. 2016. Fig. 12.

Plants medium-sized to large, in dense tufts, dim green or yellowish green above, brownish below, dull. *Stems* to 3.5 cm long, erect, simple or branched, without hyalodermis, with central strand. *Rhizoidal tubers* absent. *Leaves* appressed and slightly incurved when dry, erectopatent to patent when wet, from ovate base abruptly narrowed into narrow triangular acumina, acuminate, not decurrent, 1.8–2.7×0.6–0.9 mm, canaliculate distally; margins narrowly recurved at proximal 1/2, unistratose, entire; *costa* strong, 60–100 mm wide at leaf base, weakly narrowed upwards, percurrent or ending few cells below apex, on dorsal side prominent, on ventral side flat or weakly convex, on both sides with quadrate, smooth cells, without band of translucent cells on ventral side below apex, in transverse section semicircular, with 4–6 guide cells in 1 layer, ventral stereids in 1(2) layers, ventral epidermis differentiated, with not or slightly bulging outer walls, dorsal stereids in 1–2 layers, dorsal epidermis differentiated; lamina unistratose; upper and median laminal *cells* round-quadrate, elliptic and transversely elliptic, 4–10×5–10 µm, with moderately thickened walls, on both surfaces with 1(2) simple papillae per cell; basal juxtacostal cells short rectangular, rarer quadrate, 8–45×5–10 µm, smooth, with moderately thickened, straight walls, chlorophyllose; basal marginal cells in 8–

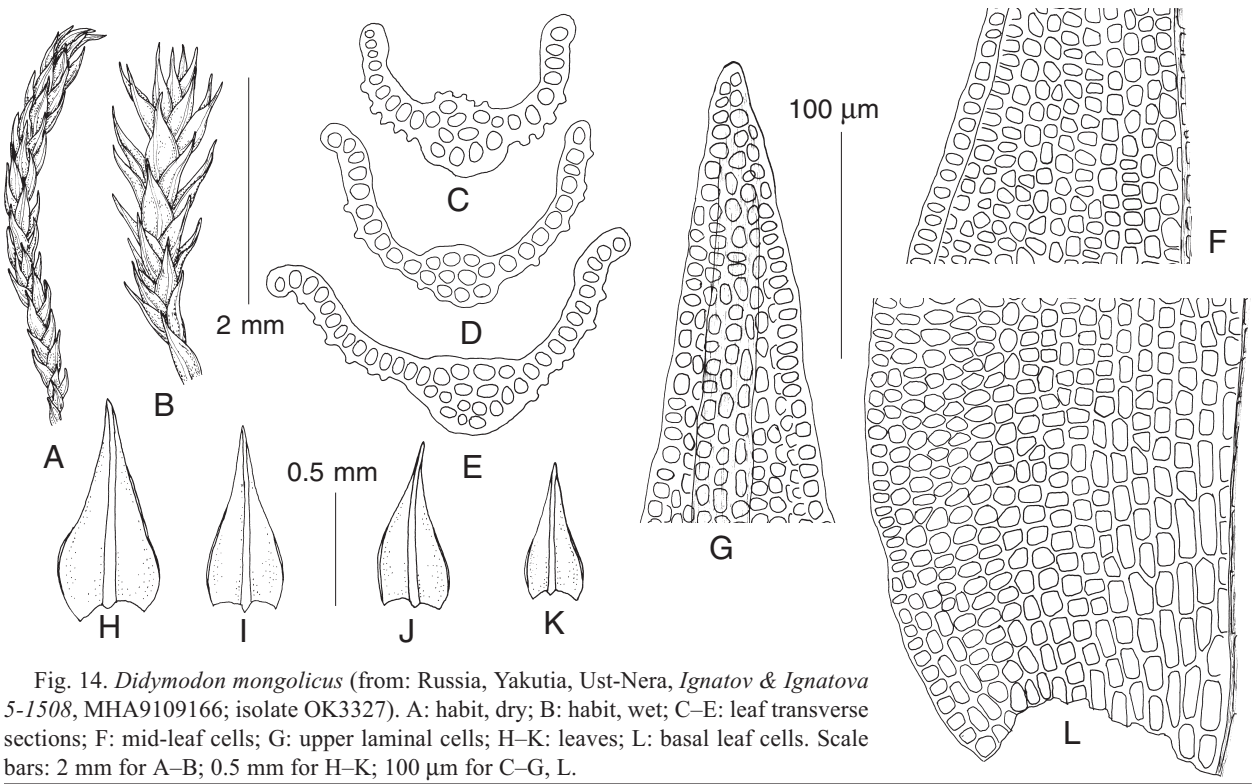

Fig. 14. *Didymodon mongolicus* (from: Russia, Yakutia, Ust-Nera, *Ignatov & Ignatova 5-1508*, MHA9109166; isolate OK3327). A: habit, dry; B: habit, wet; C–E: leaf transverse sections; F: mid-leaf cells; G: upper laminal cells; H–K: leaves; L: basal leaf cells. Scale bars: 2 mm for A–B; 0.5 mm for H–K; 100 µm for C–G, L.

10 rows quadrate and transversely rectangular. KOH-reaction yellow. *Specialized asexual reproduction* absent. *Dioicous. Perigonia* terminal. *Setae* 8–10 mm, reddish-brown. *Capsules* ovate-cylinfric, ca. 2 mm long, brown. *Opercula* high conic, ca. 1 mm long. *Peristome* on very low basal membrane, teeth 32, 1100 µm long, spirally twisted, pale reddish, papillose. *Spores* 14–16 µm.

This species in currently known from few localities in China (Yunnan and Sichuan) and from two localities in Russia: Sedaya Mt. in Primorsky Territory and Slyudyanka River valley in Irkutsk Province. It was collected on rocky soil at roadside and on blocks of marble in a quarry. It can be distinguished from *D. validus* in having sparsely papillose laminal cells (versus smooth).

7. **Didymodon daqingii** J. Kou, R.H. Zander & C. Feng, Ann. Bot. Fenn. 56: 88. 2019. Fig. 13.

Plants medium-sized, in compact tusts, olivaceous-green or brownish, dull. *Stems* 1–2 cm long, erect, simple or branched, without hyalodermis, with central strand. *Rhizoidal tubers* absent. *Leaves* flexuose when dry, patent to squarrose when wet, from ovate base abruptly narrowed into long lanceolate to subulate acumina, widely canaliculate distally, not decurrent, 2.0–2.9×0.4–0.5 mm; margins weakly recurved in proximal 1/2–3/4, entire, bistratose in upper third of leaf; costa strong, 75–100 µm wide at leaf base, weakly narrowing upwards, excurrent into a long, fragile, chlorophyllose awn, prominent dorsally, flat ventrally, on both surfaces with quadrate cells, on ventral side smooth or papillose, on dorsal side smooth, in transverse section semicircular, ventral epidermis differentiated, with outer walls not bulging, without band of translucent cells on ventral side below apex, with guide cells in 2–3 layers, ventral stereids absent, dorsal stereids in 1–3 layers, dorsal epidermis differentiated; lamina mainly unistratose, occasionally with bistratose patches in distal third; upper and median laminal *cells* rounded-quadrate and transversely rhomboidal, with angular lumina, 5–10×4–8 µm, smooth or with low, flat papillae; basal juxtacostal cells rectangular, 17–30×6–10 µm, with moderately thickened, straight walls, basal marginal cells slightly shorter. KOH-reaction yellowish-green. *Specialized asexual reproduction* absent. *Dioicous*. *Sporophytes* unknown.

This species is known from China, Inner Mongolia. We refer to it specimens from Altai and Tyva Republics in southern Siberia and from Suntar-Khayata Mt. Range in Yakutia (see also Discussion on page 137). It was collected on vertical rock outcrops on steppe slope with bushes; on boulders in dry stream bed; on wet, sunny rock outcrops on steep xeric slope; and on rock outcrops on steep forested slope to the flood valley of small river. *Didymodon daqingii* can be recognized by combination of leaves with long, subulate acumina and long excurrent costae, bistratose leaf margins, occasional bistratose patches in upper leaf lamina, guide cells in 2–3 layers and absence of ventral stereids in transverse sections of costae. Kou *et al*. (2019) describe its laminal cells as low papillose, but in their illustrations there are no true papillae but cells have slightly bulging and thickened outer walls.

8. **Didymodon mongolicus** D.P. Zhao & T.R. Zhang, Bangladesh J. Pl.Taxon. 23(2): 175. 2016. Fig. 14.

Plants small, in dense tufts, brownish-green or brown, dull. *Stems* to 3 cm long, erect, simple or branched, with-

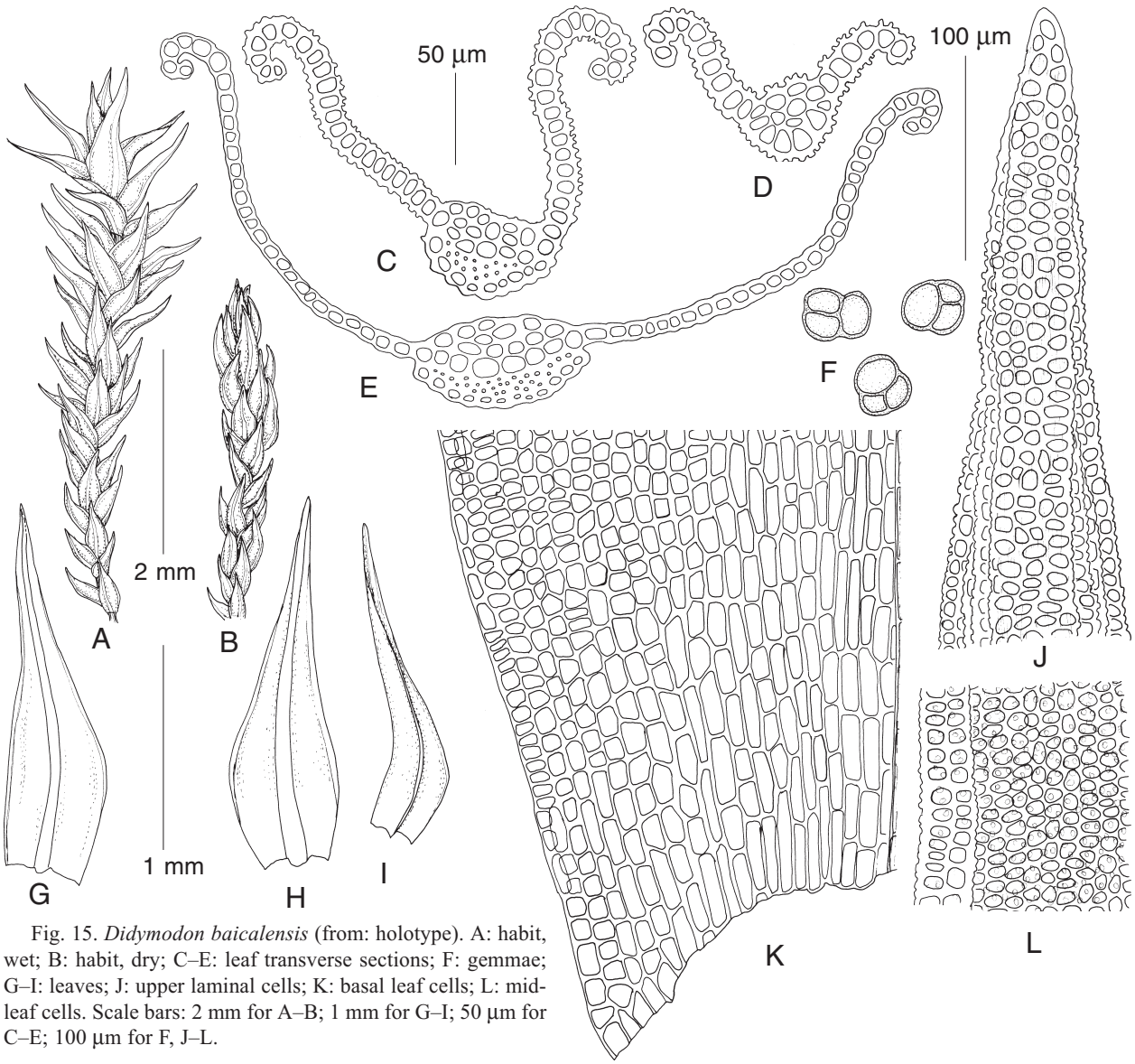

Fig. 15. *Didymodon baicalensis* (from: holotype). A: habit, wet; B: habit, dry; C–E: leaf transverse sections; F: gemmae; G–I: leaves; J: upper laminal cells; K: basal leaf cells; L: mid-leaf cells. Scale bars: 2 mm for A–B; 1 mm for G–I; 50 µm for C–E; 100 µm for F, J–L.

out hyalodermis, with central strand. *Rhizoidal tubers* absent. *Leaves* erect and appressed when dry, erectopatent when wet, ovate to ovate-lanceolate, with wide bases and short acumina, narrowly acute, not decurrent, 0.5–1.3 ×0.25–0.5 mm, canaliculate distally; margins narrowly recurved in proximal 1/2–2/3, unistratose, entire; *costa* 25–60 µm wide at leaf base, weakly narrowing upwards, percurrent, prominent dorsally, flat or slighly concave ventrally, on both surfaces with quadrate, smooth or papillose cells, without band of translucent cells on ventral side below apex, in transverse section semicircular or almost circular, with 3–5 guide cells in 1 layer, ventral stereids in 0–1 layers, ventral epidermis differentiated, with flat or slightly bulging outer walls, dorsal stereids or substereids in (0)1–2 layers, dorsal epidermis differentiated; lamina unistratose; upper and median laminal *cells* rounded-quadrate, short rectangular and transversely rectangular, 7–11×7–10 µm, with moderately thickened walls, smooth on both surfaces or on dorsal surface with 1–2 simple papillae per cell; basal juxtacostal cells short rectangular and quadrate, 13–30×7–9 µm, with moderately thickened, straight walls, smooth, chlorophyllose; basal marginal cells in 8–9 rows quadrate and transversely rectangular. KOH-reaction yellowish or orange. *Specialized asexual reproduction* absent. *Dioicous*. *Perigonia* not seen. Perichetia terminal. *Sporophytes* unknown.

Didymodon mongolicus is known from China (Inner Mongolia) and Mongolia; in the present study its presence in southern Siberia, Yakutia, and Dagestan is confirmed. Its Chinese and Mongolian plants have leaves with smooth cells, whereas in populations from Russia plants both with smooth and papillose on dorsal surface cells were revealed. Plants with papillose on dorsal suface leaf cells resemble *D. tibeticus* and *D. icmadophilus*. However, *D. tibeticus* is a smaller plant with leaves to 0.45 mm long, having flat margins, and *D. icmado-*

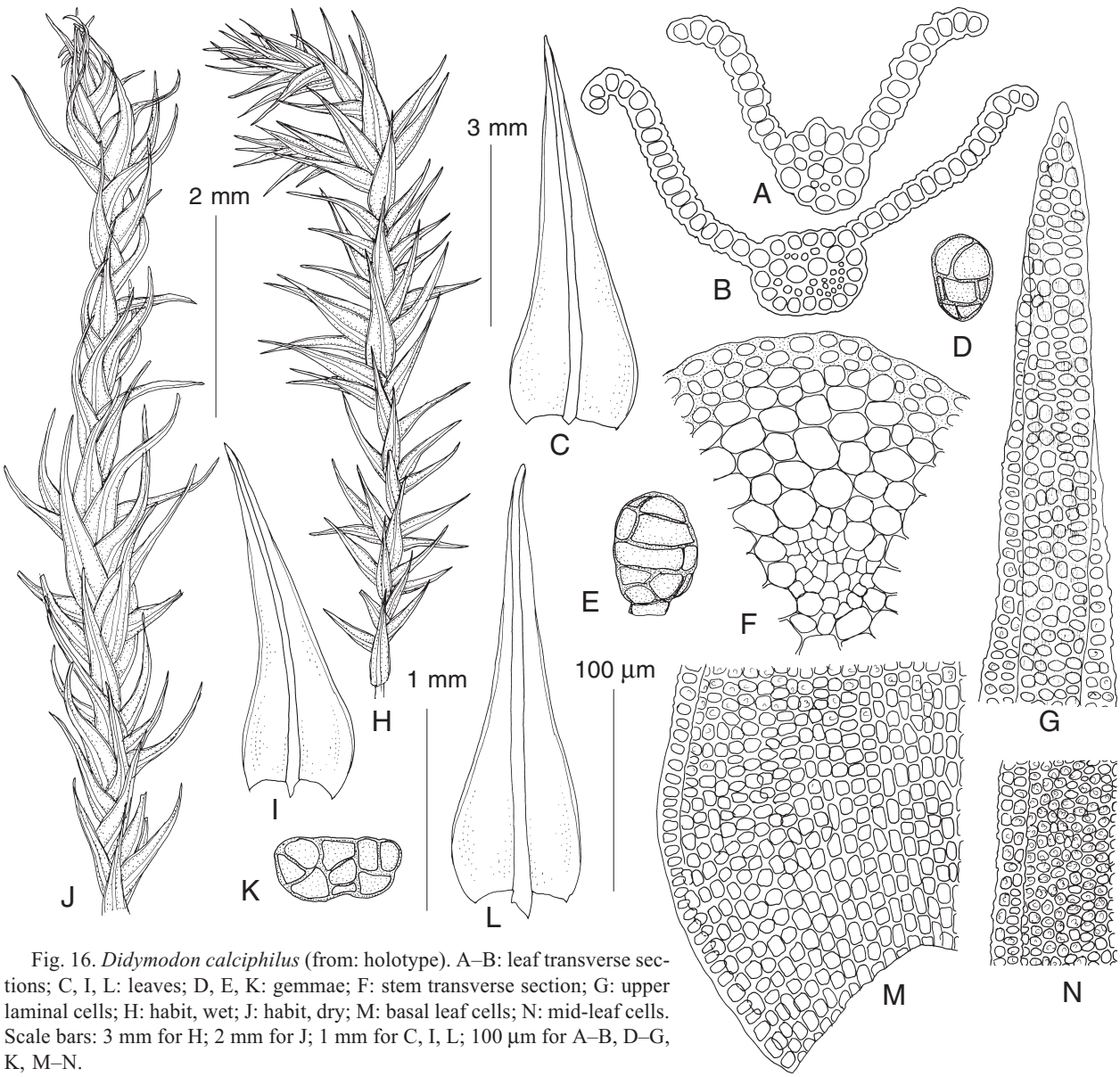

Fig. 16. *Didymodon calciphilus* (from: holotype). A–B: leaf transverse sections; C, I, L: leaves; D, E, K: gemmae; F: stem transverse section; G: upper laminal cells; H: habit, wet; J: habit, dry; M: basal leaf cells; N: mid-leaf cells. Scale bars: 3 mm for H; 2 mm for J; 1 mm for C, I, L; 100 µm for A–B, D–G, K, M–N.

philus has wider leaf bases and long excurrent costae.

9. **Didymodon baicalensis** Ignatova & Ignatov, species nova. Fig. 15.

Type: Russia, Irkutsk Province, Irkutsk District, Listvyanka, ca. 51°50'N, 104°53'E, 500 m alt., Great Baikal Trail near its starting point at Listvyanka settlement, dry rock outcrops, 10 September 2018*, Ignatov, Ignatova & Kolesnikova 18-4666* (holotype MHA9027319, isotype MW9090865).

Etymology: species name corresponds to its type locality, slopes to Baikal Lake where the Great Baikal Trail runs.

Plants small to medium-sized, in dense tufts, dark-green or brownish-green, dull. *Stems* to 3 cm long, erect, simple or branched, without hyalodermis, with central strand. *Rhizoidal tubers* absent. *Leaves* straight, appressed when dry, erectopatent to patent when wet, deltoid or deltoid-lanceolate, from ovate bases gradually or abruptly narrowed into short triangular acumina, acute, not decurrent, 1.0–2.0×0.4–0.5 mm, canaliculate distally; margins narrowly revolute almost to apex or in proximal 3/4, unistratose, entire; *costa* strong, 40–50 µm wide at leaf base, weakly narrowing upwards, excurrent into short, stout mucro, strongly prominent dorsally, flat or weakly convex ventrally, on both surfaces with quadrate, papillose cells, without band of translucent cells on ventral side below apex, in transverse section semicircular, with 2–3 layers of guide cells, 3–7 cells in each layer, ventral stereids absent, occasionally 1 layer of substereids present, ventral epidermis differentiated, with flat or slightly bulging outer walls, dorsal stereids in 2–3 layers, dorsal epidermis differentiated; lamina unistratose; upper and median laminal *cells* rounded-quadrate, elliptic and transversely elliptic, 7–10×7–10 µm, with moderately thickened walls, on both surfaces with 2–3 bifid papillae per cell; basal juxtacostal cells quadrate and short rectangular, 10–25×7–

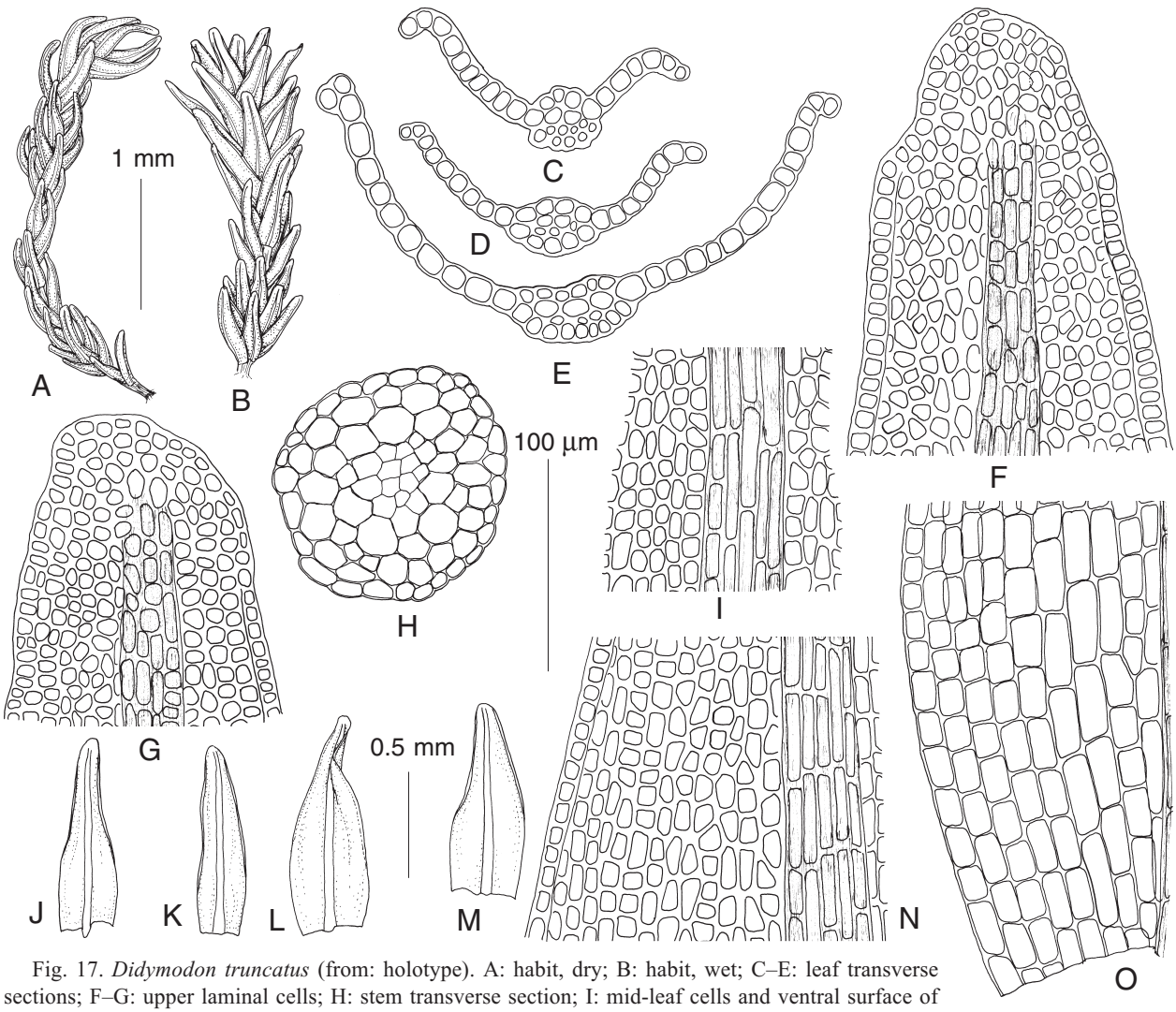

Fig. 17. *Didymodon truncatus* (from: holotype). A: habit, dry; B: habit, wet; C–E: leaf transverse sections; F–G: upper laminal cells; H: stem transverse section; I: mid-leaf cells and ventral surface of costa; J–M: leaves; N: mid-leaf cells; O: basal leaf cells. Scale bars: 1 mm for A–B; 0.5 mm for G–M; 100 µm for C–I, N–O.

10 µm, smooth, with moderately thickened, straight walls, chlorophyllose; basal marginal cells in 3–4 rows quadrate and transversely rectangular. KOH-reaction green or orange. *Asexual reproduction* by round multicellular gemmae 20–25 µm in diameter, born on branched stalks in leaf axils. *Gametangia* and *sporophytes* unknown.

Didymodon baicalensis occurs in southern Siberia (Irkutsk Province, Buryatia, Zabaikalsky Territory, Khakassia, and Altai Republic). It grows on rock outcrops and rocky soil on exposed xeric slopes and in larch forests. Some its specimens were stored in herbaria under the name *D. cordatus*. It shares with this species leaf shape, leaf margins revolute almost to apices, papillose laminal cells, and presence of multicellular axillary gemmae, but differs from it in costa structure: in *D. baikalensis*, there are 2–3 layers of guide cells but no ventral stereids, whereas in *D. cordatus* guide cells are 1-layered and ventral stereids present. Costa structure similar to *D. baicalensis* is characteristic of *D. desertorum*, but this species has smooth laminal cells.

10. **Didymodon calciphilus** Ignatova & Ignatov, species nova. Fig. 16.

Type: Russian Far East, Primorsky Territory, Partizansk District, Lozovyj (Chandolaz) Range, 43°00'N, 133°00', 360 m alt., foothills, rock outcrops in oak forest, 26 August 2007 *Ignatov 07-83* (holotype MHA9108971, isotype MW9036162).

Etymology: species name refers to its substrate preferences.

Plants medium-sized to large, in dense tufts, rigid, green or dark-green, dull but with shiny costae. *Stems* to 3 cm long, erect or ascending, simple or repeatedly branched, without hyalodermis, with large central strand. *Rhizoidal tubers* absent. *Leaves* slightly flexuose and incurved when dry, erectopatent in distal part of stem, below with appressed bases and widely spreading acumina when wet, from ovate, scarcely differentiated bases gradually or ±abruptly narrowed into triangular acumina 1.5–2 times longer than bases, acute, not or short decurrent, (1.3–)1.5–1.9×(0.3–)0.5–0.55 mm, widely keeled or al-

most flat distally; margins narrowly recurved in proximal 1/2–4/5, unistratose, entire; *costa* 65–75 μm wide at leaf base, gradually narrowing upwards, percurrent, strongly prominent dorsally, flat ventrally, on both surfaces with quadrate, smooth cells, without band of translucent cells on ventral side below apex, in transverse sections semicircular, with 3–5 guide cells in 1 layer, ventral stereids in 1(2) layers, ventral epidermis differentiated, with outer walls not bulging, dorsal stereids in 1–3 layers, dorsal epidermis differentiated; lamina unistratose; upper and median laminal *cells* rounded-quadrate, elliptic and transversely elliptic, 5–8×4–7 μm, thick-walled, on both surfaces with low, simple or bifid papillae; basal juxtacostal cells rectangular, 12–20×7–9(–11) μm, smooth, with moderately thickened, straight walls; basal marginal cells quadrate. KOH-reaction yellowish-green. *Asexual reproduction* by ovate and round multicellular gemmae on branched stalks in leaf axils. *Gametangia* and *sporophytes* unknown.

This species is currently known from Lozovyj Range in Primorsky Territory and from Gunib District in Dagestan. It grows on dry calcareous rocks. It can be recognized by combination of rigid, dark-green plants, leaves usually gradually tapered from ovate base into triangular acumina, narrowly recurved margins, papillose laminal cells, and ovate, multicellular gemmae. It differs from *D. cordatus* in different leaf shape, with scarcely differentiated bases and recurved but not strongly revolute leaf margins. From *D. baicalensis* it can be separated by costa with one layer of guide cells and ventral stereids present.

11. **Didymodon truncatus** Ignatova & Ignatov, species nova. Fig. 17.

Type: Russia, Altai Republic, Kosh-Agach District, Yuzhno-Chuisky Range, valley of Tarkhata River, along small creek – its right tributary, 49°37’32”N, 88°27’24”E, 2240 m alt., dry cliffs, in small cracks, 21 June 2021, *Ignatov & Ignatova 21-450* (holotype MHA9131861).

Etymology: name of this species reflects its often truncate leaf apices.

Plants small, in dense, soft tusfts, yellowish-green above, light brownish below, dull. *Stems* 3–5 mm long, erect, simple, without hyalodermis, with central strand. *Rhizoidal tubers* absent. *Leaves* slighly incurved when dry, erectopatent when wet, ovate or ovate-lanceolate, with weakly differentiated bases, gradually tapered into acumina, widely rounded or truncate at apices, not decurrent, 0.55–1.0×0.22–0.28 mm, concave distally; margins narrowly recurved from proximal 1/3 almost to apex, unistratose, entire; *costa* 30–50 μm wide at leaf base, slightly narrowing upwards, percurrent or ending few cells below apex, weakly prominent dorsally, flat or convex ventrally, sharply delimited from laminal cells, on both surfaces with elongate rectangular, smooth cells, without band of translucent cells on ventral side below apex, in transverse section semicircular or round, with 2–3 guide cells in 1 layer, ventral stereids absent, ventral epidermis differentiated, with outer walls not bulging, dorsal substereids in 1 layer, dorsal epidermis differentiated; lamina unistratose; upper and median laminal *cells* irregularly polygonal, 8–17×9–12 μm, thick-walled, smooth; basal juxtacostal cells rectangular, 11–30×6–9 μm, smooth, with moderately thickened, straight walls, hyaline; basal marginal cells in 3–4 rows shorter, short rectangular. KOH-reaction yellowish-green. *Specialized asexual reproduction* absent. *Gametangia* and *sporophytes* unknown.

This species is currently known only from type locality. There is some similarity between *D. truncatus* and *Geheebia tophacea* in elongate, smooth ventral cells of costa and leaves with rounded apices. However, plants of *G. tophacea* are larger, with leaves 1.0–2.2×0.3–0.4 (–0.8) mm vs 0.55–1.0×0.22–0.28 mm in *D. truncatus*, decurrent at base, with narrower acumina, and laminal cells with low papillae (smooth in *D. truncatus*).

KEY TO IDENTIFICATION OF *DIDYMODON* S. STR. IN RUSSIA

1. Leaves fragile; leaf apices caducous, differentiated into swollen, rhomboidal propagula consisting entirely of the costa ..... *D. anserinocapitatus*
— Leaves not fragile or, rarely, with leaf tips broken off but not differentiated into propagulae 2
2. Plants bluish green; leaves linear-lanceolate, usually crisped when dry; basal laminal cells strongly differentiated, hyaline, thin-walled ..... *D. glaucus*
— Plants green, yellowish-green or brown; leaves ovate, ovate-lanceolate, or lineaer-lanceolate, not crisped when dry; basal cells not or weakly differentiated, firm-walled 3
3. Leaf margins crenulate by bulging cell walls 4
— Leaf margin smooth 6
4. Upper leaf cells covered with low and flattened papillae visible only in leaf transverse section; gemmae absent ..... *D. nigrescens*
— Leaf cells smooth; unicellular gemmae occasionally present 5
5. Plants with fragile flagelliform innovations; leaves dimorphic ..... *D. subandreaeoides*
— Plants without fragile flagelliform innovations; leaves monomorphic ..... *D. perobtusus*
6. Ventral (adaxial) surface cells of costa in the upper half of leaf elongated, not transient from lamina 7
— Ventral (adaxial) surface cells of costa in the upper half of leaf ± isodiametric, transient from lamina 8
7. Leaves ovate-lanceolate, acuminate, catenulate when dry; multicellular gemmae usually present in leaf axils ..... *D. maschalogena*
— Leaves ovate, truncate at apices, not catenulate when dry; gemmae absent ..... *D. truncatus* (p. 152)
8. Upper leaf margins regularly bistratose in 1–3 cell rows 9
— Upper leaf margins unistratose 10

9. Leaf apices not sharp; costa not sharply delimited from the lamina in distal part of leaf acumen, percurrent ..... *D. rigidulus*
— Leaf apices sharp; costa sharply delimited from the lamina, long excurrent ..... *D. daqingii* (p. 148)
10. Laminal cells smooth 11
— Upper and median laminal cells papillose on both surfaces or only on dorsal side 15
11. Costae long excurrent; leaf tips fragile, often broken off ..... *D. abramovae* (p. 144)
— Costa percurrent or short excurrent; leaf tips not fragile 12
12. Leaves 1.6–3.2 mm long, with acumina longer than bases ..... *D. validus* (p. 140)
— Leaves 0.4–1.8 mm long, with acumina equal in length to bases or slighly longer 13
13. Leaves 0.8–1.8×0.3–0.65 mm; laminal cells thick-walled, with rounded lumens ..... *D. acutus*
— Leaves 0.5–1.3×0.25–0.5 mm; laminal cells thin-walled or with moderately thickened walls, with subquadrate, rectangular or ovate lumens 14
14. Leaves 0.6–0.85×0.25–0.3 mm; in mesic habitats . ..... *D. borealis* (p. 141)
— Leaves 0.5–1.3×0.4–0.5 mm; in xeric habitats .... *D. mongolicus* p.p. (p. 148)

15(10). Upper and median laminal cells equally papillose on both surfaces 16
— Upper and median laminal cells papillose only or predominantly on dorsal surface, occasionally with few papillae on ventral side 22
16. Leaf margins recurved at lower 1/2–3/4, rarely almost to the apex 17
— Leaf margins revolute almost to apex 20
17. Upper leaves erectopatent when wet, with weakly differentiated bases, gradually narrowed into acumina; upper and median laminal cells densely papillose, papillae simple and bifid ... *D. calciphilus* (p. 151)
— Leaves widely spreading to squarrose when wet, gradually or abruptly narrowed into long acumina (longer than bases); upper and median laminal cells with sparse, simple papillae 18
18. Leaves with narrow bases, 0.3–0.35 mm wide, from short-rectangular bases gradually narrowed into acumina, to 1.9 mm long ..... *D. cherdantsevae* (p. 145)
— Leaves with wider bases, 0.6–0.9 mm wide, from ovate bases ±abruptly narrowed into acumina, to 3.2 mm long 19
19. Leaves 1.8–2.7×0.6–0.9 mm; costa percurrent; leaf margins recurved to 3/4 of leaf length; gemmae absent ..... *D. hengduanensis* (p. 147)
— Leaves 1.5–3.2×0.5–0.8 mm; costa excurrent; leaf margins recurved almost to the apex; ovate multicellular gemmae often present in leaf axils .... [*D. schensianus*]

20(16). Costa in transverse section with guide cells in 2-3 layers, without ventral stereids .... *D. baicalensis* (p. 149)
— Costa in transverse section with guide cells in 1 layer, ventral stereid band present 21
21. Leaves with cordate bases ..... *D. cordatus*
— Leaves with square bases ..... [*D. tectorum*]

22(15). Plants tiny, leaves to 0.45 mm long, with flat margins ..... *D. tibeticus*
— Plants larger, leaves longer than 0.45 mm, with narrowly recurved margins 23
23. Costa long-excurrent ..... *D. icmadophilus* (p. 142)
— Costa percurrent to short-excurrent .... *D. mongolicus* p.p. (p. 148)

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Appendix 1. Specimen voucher information and GenBank accession numbers for the newly obtained sequences of *Didymodon*.

Species	Isolate	Location	Specimen voucher	ITS	trnG
D. abramovae	OK3449	Russia: Dagestan, Gunib Distr.	Ignatov Ignatova 09-607, MHA9101354	PQ807434	PQ778365
D. abramovae	OK3454	Russia: Yakutia, Ulakhan-Chistai	Ignatov & Ignatova 18-2155, MHA9028926	PQ807436	PQ778367
D. abramovae	OK4108	Russia: Tyva	Pisarenko 23/42, MHA	PQ807433	PQ778364
D. cf. *abramovae*	OK3451	Russia: Ingushenia	Ignatov et al. 18-538, MHA9026616	PQ807435	PQ778366
D. cf. *abramovae*	OK3452	Russia: Perm Territory	Bezgodov 441, 16 Aug 2014, MHA9018160	PQ807437	PQ778372
D. cf. *abramovae*	OK4112	Russia: Tyva	Pisarenko 23/3, MHA	PQ807432	PQ778371
D. baicalensis	OK3321	Russia, Irkutsk Province	Ignatov et al., 18-4666, MHA9027319	PQ807457	-
D. baikalensis	OK3457	Russia: Altai Republic, Tabozhok	Ignatov 30/101, MHA	PQ807456	PQ778387
D. baikalensis	OK3474	Russia: Khakasia	Ignatov & Spirina 11-5041, MHA9102579	PQ807452	PQ778384
D. baikalensis	OK3475	Russia: Irkutsk Province	Ignatov et al. 18-4691, MHA91027313	PQ807455	PQ778386
D. baikalensis	OK3489	Russia: Zabaikalsky Territory	Afonina 30907, LE	PQ807453	PQ778385
D. baikalensis	OK3496	Russia: Buryatia	Afonina 16-22a, LE	PQ807454	-
D. baikalensis	OK3519	Russia, Buryatia	Afonina 01008, LE	PQ807459	PQ778389
D. baikalensis	OK4103	Russia: Irkutsk Province	Ignatov et al. 18-4666, MHA9027319	PQ807458	PQ778388
D. borealis	OK3320	Russia, Yakutia, Sette-Daban	Ignatov & Ignatova 17-426, MHA9025679	PQ807442	-
D. borealis	OK3329	Finland	Ignatov & Ignatova 10-1004, MHA9066377	PQ807444	PQ778376
D. borealis	OK4106	Russia: Perm Territory	Bezgodov 87, 20 June 2012, MHA9120546	PQ807445	PQ778377
D. calciphilus	OK3455	Mongolia	Ignatov 01-232, MHA	PQ807451	PQ778383
D. calciphilus	OK4053	Russia: Primorsky Territory, Lozovyj Range	Ignatov 07-83, MHA9108971	PQ807489	PQ778409
D. calciphilus	OK4101	Russia: Primorsky Territory, Lozovyj Range	Ignatov 07-46, MHA9108966	PQ807490	PQ778410
D. calciplilus	OK3477	Russia, Dagestan, Gunib Distr.	Ignatov & Ignatova 09-117, MHA9101317	PQ807488	PQ778408
D. cherdantsevae	OK4019	Russia: Primorsky Territory, Popova Island	Fedosov 24-351 14 Sept 2024, MW9092502	PQ807496	PQ778417

Species	Isolate	Location	Specimen voucher	ITS	trnG
D. cherdantseviae	OK3317	Russia: Primorsky Territory, Sedaya Mt.	Ignatov & Ignatova 13-1549, MHA9109146	PQ807497	PQ778418
D. cordatus	OK3473	Russia: Primorsky Territory, Sedaya Mt.	Ignatov & Ignatova 13-1535, MHA9101327	PQ807491	PQ778411
D. cordatus	OK3476	Russia: Dagestan, Keger	Ignatov & Abakarova 11-178, MHA9101318	PQ807492	-
D. cordatus	OK3488	Russia: Altai, Chulyshman	Ignatov & Ignatova 12-531, MHA9101323	PQ807493	PQ778412
D. daqingii	OK3467	Russia: Yakutia, Suntar-khayata	Ignatov Ignatova 15-934, MHA9101345	PQ807446	PQ778378
D. daqingii	OK3470	Russia: Yakutia, Suntar-khayata	Ignatov et al. 15-11, MHA9108739	PQ807447	PQ778379
D. daqingii	OK4061	Russia: Yakutia, Suntar-Khayata	Ignatov & Ignatova 15-934, MHA9101345	PQ807448	PQ778380
D. daqingii	OK4062	Russia: Yakutia, Suntar-Khayata	Ignatov & Ignatova 15-11, MHA9108739	PQ807449	PQ778381
D. daqingii	OK4111	Russia: Tyva	Pisarenko 23/17, MHA	PQ807450	PQ778382
D. glaucus	OK4066	Russia: Altai, Inya	Ignatov & Ignatova 21-214 MHA9130603	PQ807498	PQ778419
D. hengduanensis	OK3326	Russia: Primorsky Territory, Sedaya Mt.	Ignatov & Ignatova 13-1517, MHA9109153	PQ807440	PQ778373
D. hengduanensis	OK4058	Russia: Irkutsk Province	Ignatov et al. 18-4492, MW9090873	PQ80744	PQ778374
D. icmadophilus	OK4057	Russia: Karachaevo-Cherkessian Rep, Teberda	Ignatov & Ignatova 05-3531, MW9035941	PQ807439	PQ778369
D. mongolicus	OK3312	Russia, Dagestan, Gunib Distr.	Ignatov & Ignatova 09-682, MHA9109100	PQ807463	-
D. mongolicus	OK3313	Russia: Dagestan, Charoda Distr.	Ignatov & Abakarova 11-227, MHA9109119	PQ807464	PQ778390
D. mongolicus	OK3315	Russia, Altai, Ust-Kan	Ignatov & Ignatova 12-671, MHA9109126	PQ807465	-
D. mongolicus	OK3316	Russia, Altai, Kaitanak	Ignatov & Ignatova 12-818, MHA9109134	PQ807467	-
D. mongolicus	OK3327	Yakutia, Ust-Nera	Ignatov & Ignatova 15-1508, MHA9109166	PQ807461	-
D. mongolicus	OK3404	Russia, Buryatia	Afonina 1222, LE	PQ807460	-
D. mongolicus	OK3453	Russia: Dagestan, Gunib Distr.	Ignatov & Ignatova 09-100, MHA9101352	PQ807466	PQ778391
D. mongolicus	OK4107	Russia, Tyva	Pisarenko 23/15, MHA	PQ807462	-
D. mongolicus	OK4113	Russia, Tyva	Pisarenko 23/7, NSK, MHA	PQ807468	PQ778392
D. rigidulus	OK3520	Russia, Sakhalin	Pisarenko 03959, NVS	PQ807431	PQ778363
D. tectorum	OK3482	Russia: Altai, Chegan-Uzun	Ignatov & Ignatova 12-481, MHA9109190	PQ807495	PQ778415
D. tibeticus	OK4071	Russia: Zabaikalsky Territory	Afonina 62-13, LE	PQ807438	PQ778368
D. truncatus	OK3893	Russia: Altai, Yuzhno-Chuisky Range	Ignatov & Ignatova 21-450, MHA	PQ807494	PQ778414
D. validus	OK3308	Russia, Chelyabinsk Province	Ibatullin 44/2.2, MHA9101306	PQ807469	-
D. validus	OK4104	Russia, Altai Republic, Tabozok	Ignatov & Ignatova 21-596, MHA9131062	PQ807483	PQ778416
D. validus	OK3310	Russia: Kursk Provimce	Popova 66, 8 Sept 2014, MHA9109091	PQ807470	PQ778403
D. validus	OK3311	Russia: Sverdlovsk Province	Bezgodov 15, 11 July 2017, MHA9049397	PQ807443	PQ778375
D. validus	OK3314	Russia: Ingushetia	Ignatov et al. 18-1094, MHA9016027	PQ807471	PQ778397
D. validus	OK3318	Russia: Primorsky Territory, Lozovyj Range	Ignatov et al. 13-1871, MHA9109147	PQ807475	PQ778401
D. validus	OK3319	Russia: Yakutia, Nizhny Bestyakh	Ignatov & Ignatova 18-2972, MHA9029434	PQ80747	PQ778398
D. validus	OK3322	Russia: Yakutia, Sette-Daban	Ignatov & Ignatova 16-756, MHA9022026	PQ807485	PQ778407
D. validus	OK3324	Russia, Amurskaya Province	Bezgodov 353, 20 June 2011, MHA9101313	PQ807486	-
D. validus	OK3328	Russia: Khabarovsk Province, Ayan	Klimova & Bakalin, MHA9130185	PQ807480	PQ778396
D. validus	OK3463	Russia: Yakutia, Sette-Daban	Ignatov & Ignatova 15-710, MHA9101341	PQ807478	PQ778393
D. validus	OK3464	Russia: Yakutia, Ust-Nera	Ignatov & Ignatova 15-1069, MHA9101342	PQ807482	PQ778404
D. validus	OK3466	Russia: Yakutia, Sette-Daban	Ignatov & Ignatova 15-543, MHA9101343	PQ807476	PQ778402
D. validus	OK3468	Russia: Yakutia, Sette-Daban	Ignatov Ignatova 15-739 MHA9101348	PQ807484	PQ778406
D. validus	OK4054	Russia: Primorsky Territory, Nakhodka	Ignatov 08-238 MHA9109151	PQ807473	PQ778400
D. validus	OK4055	Russia: Amurskaya Province, Zeya	Dudov & Kozhin 2016_Br_0992, MW9079896	PQ807487	PQ778405
D. validus	OK4063	Russia: Altai, Chemal	Ignatov & Ignatova 29/75, MHA90101360	PQ807479	PQ778395
D. validus	OK4064	Russia: Altai, Ust-Sema	Ignatov & Ignatova 12/317, MHA90101360	PQ807477	PQ778394
D. validus	OK4072	Russia: Yakutia, Lenskie Stolby	Ignatov & Ignatova 16-385, MHA9021318	PQ807474	PQ778399
D. validus	OK4102	Russia, Primorsky Territory, Chuguevka	Ignatov 07-407, MHA9108970	PQ807481	-

For Genbank accession numbers of specimens downloaded from genbank (nr ITS region, plastid *trn*G intron, *trn*L–*trn*F region and atpB-rbcL spacer) see supplementary material at: http://arctoa.ru/ru/Archive-ru/33_2/Arctoa_33_Didymodon_SM.xlsx