

TWO NEW SPECIES OF *DIDYMODON* (POTTIACEAE, BRYOPHYTA) FROM ASIAN RUSSIA  
ДВА НОВЫХ ВИДА *DIDYMODON* (POTTIACEAE, BRYOPHYTA) ИЗ АЗИАТСКОЙ РОССИИ

ELENA A. IGNATOVA<sup>1</sup>, VLADIMIR E. FEDOSOV<sup>1,2</sup>, ALINA V. FEDOROVA<sup>3</sup>,  
OXANA I. KUZNETSOVA<sup>3</sup> & MICHAEL S. IGNATOV<sup>1,3</sup>

ЕЛЕНА А. ИГНАТОВА<sup>1</sup>, ВЛАДИМИР Э. ФЕДОСОВ<sup>1,2</sup>, АЛИНА В. ФЕДОРОВА<sup>3</sup>,  
ОКСАНА И. КУЗНЕЦОВА<sup>3</sup>, МИХАИЛ С. ИГНАТОВ<sup>1,3</sup>

Abstract

An additional study of the specimens of *Didymodon* using a morpho-molecular approach resulted in the description of two species new to science from Asian Russia. *Didymodon ussuriensis* was described from the southern Russian Far East (Ussurijsky Reserve) and found also in Amur Province (Tukuringra Range) and Zabaikalsky Territory. *Didymodon sibiricus* was described from Yakutia (Suntar Khayata Range); it was also found in Taimyr Peninsula (Byrranga Range) and southern Siberia (Republics Altai, Tyva, and Buryatia, Zabaikalsky Territory). Descriptions, illustrations, distribution, ecological data, and comparison with similar species are provided.

Резюме

Дополнительное изучение образцов *Didymodon* из азиатской России с помощью морфологических и молекулярно-генетических методов позволило описать два новых для науки вида. *Didymodon ussuriensis* описан с юга российского Дальнего Востока (из Уссурийского заповедника) и найден также на хребте Лозовом в Приморье, в Амурской области (на хребте Тукурингра в Зейском заповеднике) и в Забайкальском крае. *Didymodon sibiricus* описан из Якутии (хребет Сунтар-Хаята); он найден также на полуострове Таймыр (хребет Бырранга) и на юге Сибири (Алтай, Тыва, Бурятия, Забайкальский край). Приводятся описания, иллюстрации, распространение и характеристика местообитаний, а также сравнение с морфологически сходными видами.

KEYWORDS: mosses, new species, ITS, *trnG*, molecular phylogeny

INTRODUCTION

The genus *Didymodon* s.l. with hundreds of names has been recently revised worldwide by Jiménez *et al.* (2016), who split it into eight genera. Even after that, *Didymodon* s.str. remains the largest genus in this group with nearly one hundred species, i.e. more than in all seven genera segregated from it (Brinda & Atwood, 2025). The level of the *Didymodon* knowledge remains uneven across different regions of the world. Jiménez (2006) revised *Didymodon* s.l. for the territory of Europe, North Africa, and Southwest Asia, accepting 30 species, and 30 species of *Didymodon* s.l. are also listed in the Checklist of European bryophytes (Hodgetts & Lockhart, 2020). The “Moss Flora of China” (English version) includes 19 species of *Didymodon* s.l. (Li *et al.*, 2001); however, as much as 15 species of *Didymodon* were subsequently described from China (e.g., Zhao *et*

*al.*, 2014, 2016, 2018; Kou *et al.*, 2018, 2019; Wu *et al.*, 2023; Jiménez *et al.*, 2016, 2024, *etc.*), and this genus is likely awaiting a summary revision in this region.

For Russia, 22 species of *Didymodon* s.l. were reported in the Checklist of East Europe and North Asia (Ignatov *et al.*, 2006); since then, new findings (Afonina *et al.*, 2010, 2016; Ignatov *et al.*, 2024; Afonina & Ignatova, 2024) and the new species description (Afonina & Ignatova, 2007) continuously increased the number of species. The recently applied morpho-molecular study of the genus in Russia resulted in the description of 6 new species and recording of 4 species new to Russia, with clarifying the distribution of many other species of the genus (Ignatova *et al.*, 2024). This raised the diversity of *Didymodon* s.l. in Russia up to 42 species.

Most of new species were found in *Didymodon* s. str., i. e. sensu Jiménez *et al.* (2022), where many recently

<sup>1</sup> – Lomonosov Moscow State University, Faculty of Biology, Plant Ecology and Geography Dept., Leninskie Gory Str. 1–12, Moscow 119234 Russia. E-mails: arctoa@list.ru; fedosov\_v@mail.ru; misha\_ignatov@list.ru. ORCID: (EI) 0000-0001-6287-5660, (VF) 0000-0002-5331-6346, (MI) 0000-0001-6096-6315

<sup>2</sup> – Botanical Garden-Institute, Far Eastern Branch of the Russian Academy of Sciences, Makovskogo Street, 142, Vladivostok, 690024, Russia

<sup>3</sup> – Tsitsin Main Botanical Garden, Russian Academy of Sciences, Botanicheskaya Str., 4, Moscow 127276 Russia. ORCID (OK): 0000-0002-5513-1329, (AF) 0000-0001-6096-6315

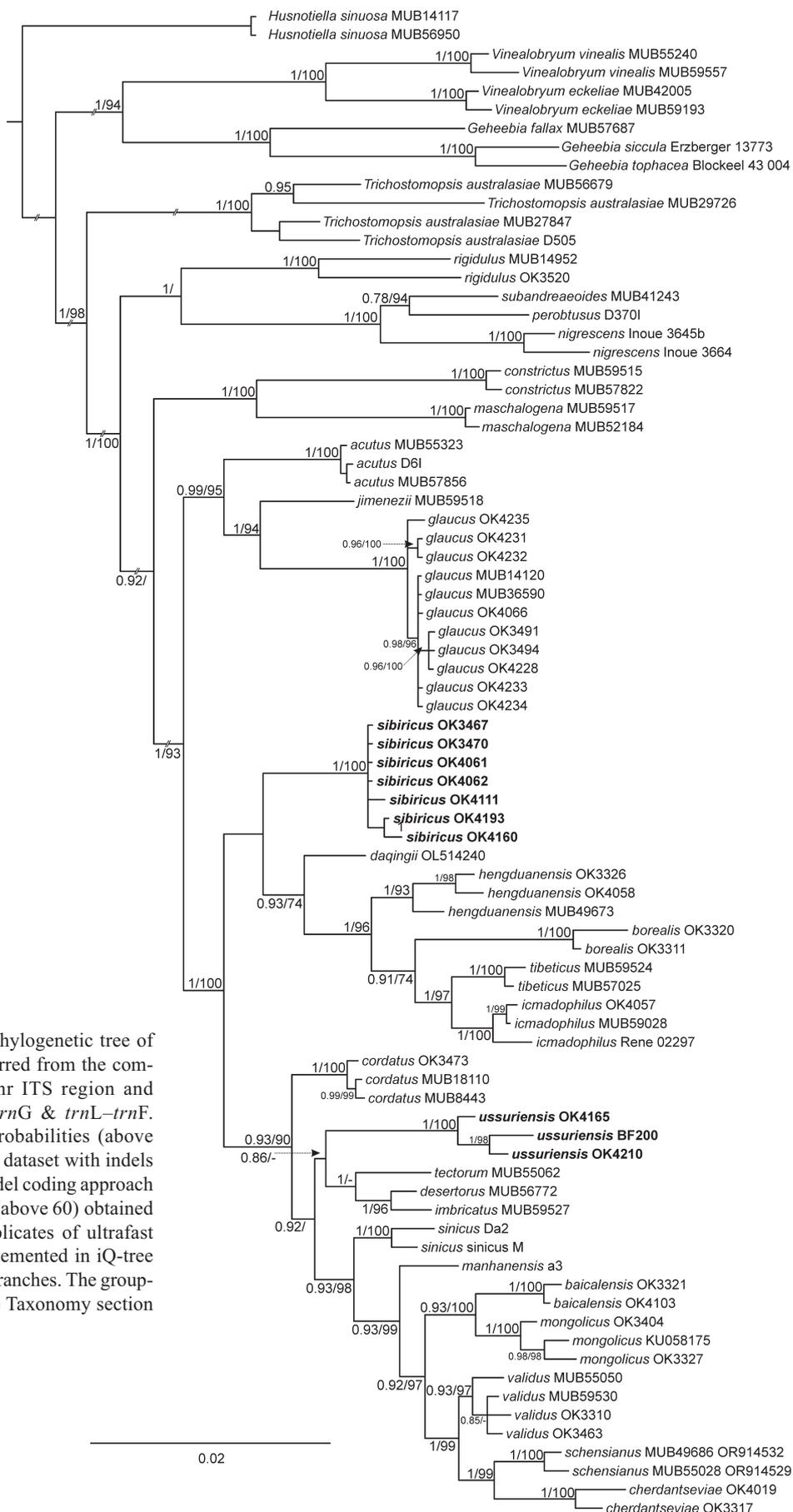


Fig. 1. Bayesian phylogenetic tree of *Didymodon* s.str. inferred from the combined sequences of nr ITS region and plastid *atpB-rbcL*, *trnG* & *trnL-trnF*. Bayesian posterior probabilities (above 0.7) inferred from the dataset with indels coded using simple indel coding approach and Bootstrap values (above 60) obtained from 1000 pseudoreplicates of ultrafast bootstrapping as implemented in iQ-tree are shown above the branches. The groupings considered in the Taxonomy section are boldfaced.

described Chinese species belong as well. This group was especially difficult due to enormous variation in their gametophyte morphology, which hampers the taxa separation without additional data from molecular markers. High molecular variation in *Didymodon* s. str. helped a lot in delimiting taxa within it; moreover, the infraspecific variation in the delimited species appeared to be relatively low and consistent with their morphology.

In the course of further identification of the abundant collections in MHA and MW, including the most problematic herbarium specimens, using the key and descriptions in Ignatova *et al.* (2024) we encountered several puzzling specimens. Therefore an additional study of them has been done using the same approach; the results of this study are presented here.

One of the objectives of the present study were three specimens similar to *Didymodon glaucus*<sup>1</sup> but differing from all other specimens from Russia in a number of features; their study includes an extended set of *D. glaucus* specimens from different regions of Russia. The second focus of the study is the specimens previously tentatively referred to *D. cf. daqingii* (Ignatova *et al.*, 2024).

#### MATERIAL AND METHODS

Protocols of DNA extracting, PCR and sequencing were essentially the same as described in the previous *Didymodon* study (Ignatova *et al.*, 2024). Newly obtained sequences were incorporated in the dataset used in that study. After first analyses performed following procedures described in Ignatova *et al.* (2024), the dataset was cut so that only groupings closely related to the taxa of the interest and those reflecting backbone phylogeny of *Didymodon* were retained. Four GenBank accessions of *Trichostomopsis* were included due to their morphological similarity with the target groups of specimens. After re-aligning, the final dataset of 82 terminals included 2653 positions, 1052 of nrITS, 1601 corresponded to the concatenation of three plastid loci, *trnG* intron, *AtpB-rbcL* spacer and *trnL-trnF* region, among which only for *trnG* intron original sequences were obtained from the target specimens. Protocols and settings of the phylogenetic analyses are the same as in Ignatova *et al.* (2024).

Specimen data and GenBank accession numbers for the newly sequenced specimens are provided in Appendix.

#### RESULTS

The trees inferred from the BA and ML analyses (Fig. 1) showed topologies similar to those presented by Ignatova *et al.* (2024); therefore, here we consider only affinities of the newly involved or reassessed groupings. Despite the sufficient variability among the ITS sequences, the accessions of *Trichostomopsis* form a completely supported clade sister to the *Didymodon* s.str. clade.

Accessions OK3467, 3470, 4061, 4062, 4111 referred

earlier to *D. cf. daqingii*, as well as newly added OK4160 and 4193 form a completely supported clade which is found in not supported sister position to the clade composed of *D. daqingii*, *D. hengduanensis*, *D. borealis*, *D. tibeticus*, and *D. icmadophilus*. This topology does not support referring specimens from Russia to *D. daqingii*, as it was tentatively done by Ignatova *et al.* (2024) due to their considerable morphological similarity to this species. However, further morphological study resulted in finding some additional distinctions between specimens from Asian Russia and *D. daqingii* described from Inner Mongolia, China. Thus, they are described below as a new species, *D. sibiricus*.

Accessions BF200, OK4165, and 4210 form a new clade as compared to the previously published topology, and its affinities within the “clade 5” (see Ignatova *et al.*, 2004) are also weakly resolved, since neither its grouping with *D. tectorum* & *D. desertorum* & *D. imbricatum* clade nor the two deeper nodes comprising it got reasonable statistical support. On the other hand, a suite of newly added Russian specimens similar in leaf shape to specimens in question but having unistratose leaf margins, OK3491, 3494, 4228, and 4231–4235, were resolved as members of the completely supported *D. glaucus* clade within the “clade 3” of *Didymodon* s.str. Thus, taking into account a separate position in the molecular phylogenetic tree and morphological distinctions of these specimens in question, we describe them below as another new species, *D. ussuriensis*.

#### TAXONOMY

***Didymodon sibiricus*** Ignatova & Fedosov, species nova. Fig. 2.

TYPE: Russia, Republic Sakha/Yakutia, Tomponsky District, Verkhoyansky Mountain system, Suntar-Khayata Range, ca. 63°07'N, 139°00'E, 980 m a.s.l., Sukhaya Creek, right bank, larch forest with *Chosenia* on low terrace, cliffs at slope base, on inclined rock surface, 23.VII.2015, Ignatov & Ignatova 15-11 (Holotype MHA9108739!, isotype MW9035965!).

**Diagnosis:** the new species is similar to *Didymodon daqingii* J. Kou, R.H. Zander & C. Feng in having leaves with long, narrow acumina and long excurrent costae, occasionally fragile, and costae lacking ventral stereids, but differs from it in smaller leaves, partially bistratose lamina not only at margins, and smooth laminal cells.

**Etymology:** the species name corresponds to Siberia, a region of northern Asia where it is distributed.

**Description.** Plants small or medium-sized, in dense tufts, dark green or brownish-green, not glossy. Stems 1.0–1.5 cm long, simple or irregularly branched, with moderately large central strand. Leaves loosely appressed and slightly flexuose when dry, widely spreading when wet, 0.8–1.8×0.3–0.4 mm, moderately fragile or, rarer, not fragile, from ovate bases gradually or ±abruptly tapered into long, linear-lanceolate acumina, canaliculate distally, not decurrent at bases; margins slightly recurved on both sides

<sup>1</sup> The authors of taxa are in accordance to Brinda & Atwood (2025), so they are omitted in the text.

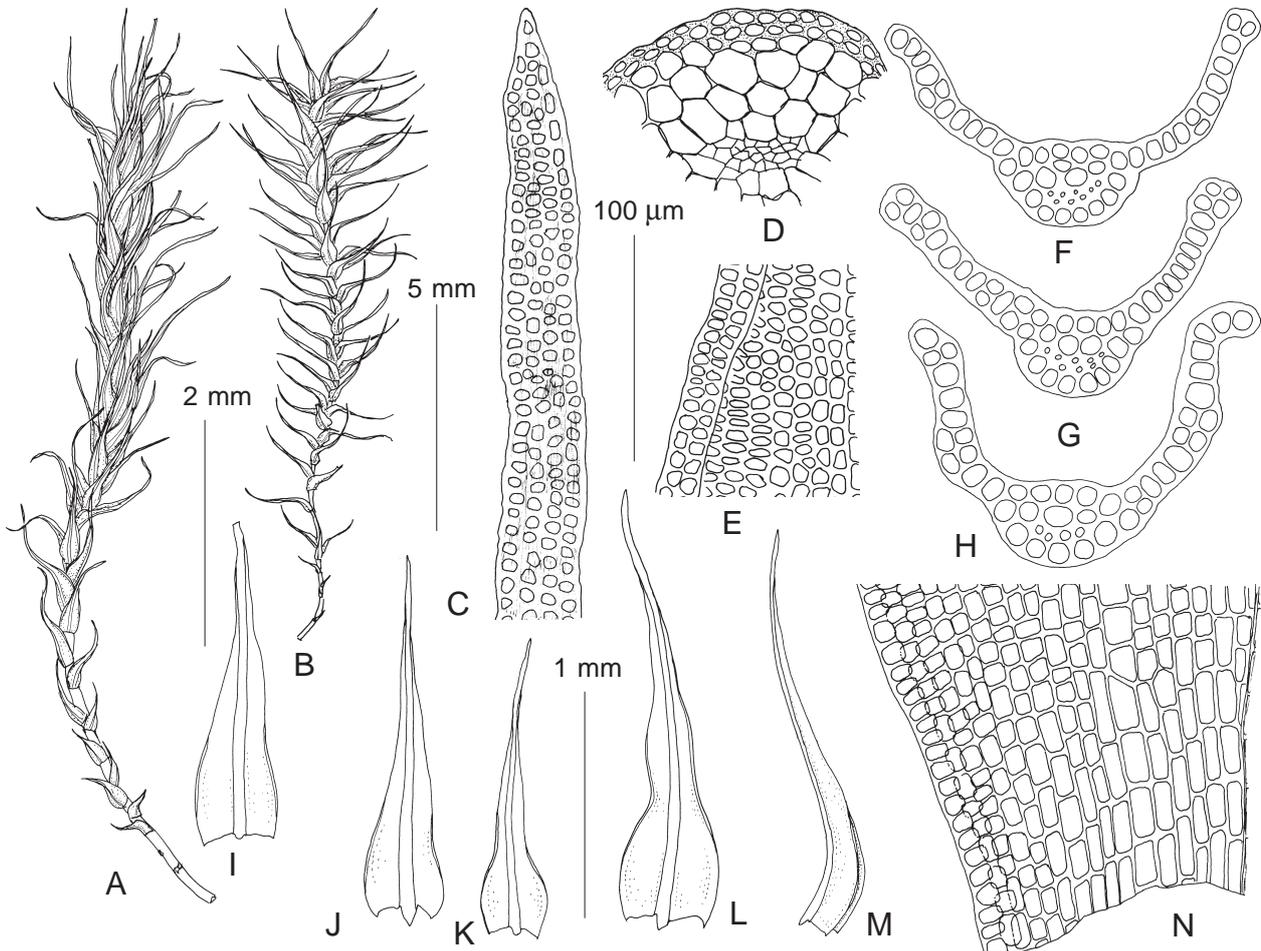


Fig. 2. *Didymodon sibiricus* Ignatova & Fedosov (from holotype). A: habit, dry; B: habit, wet; C: upper leaf cells; D: stem transverse section; E: median leaf cells; F–H: leaf transverse sections; I–M: leaves; N: basal leaf cells. Scale bars: 5 mm for B; 2 mm for A; 1 mm for I–M; 100  $\mu$ m for C–H, N.

at proximal 1/2–3/4 of leaf, entire; *costa* moderately strong, 50–75  $\mu$ m wide at leaf base, gradually narrowing upwards, long excurrent, strongly prominent dorsally, flat ventrally, with quadrate, smooth cells on both surfaces, without a pad of large, translucent cells on ventral surface below leaf apex, in transverse section semicircular, guide cells in 1–2(–3) layers, dorsal stereids in 1–3 layers, ventral stereids lacking or few substereids present in proximal part, ventral and dorsal epidermis differentiated; *lamina* partially bistratose distally at margins or near *costa*, or between *costa* and margins, unistratose in proximal part of leaf; *cells* in distal part of leaf rounded-quadrate and oblate, with angular lumina, 5–10 $\times$ 4–8  $\mu$ m, smooth; basal leaf cells weakly differentiated, in few rows short rectangular, 15–25 $\times$ 6–10  $\mu$ m, basal marginal cells quadrate and oblate. *KOH* reaction yellowish-green. *Brood bodies* absent. *Dioicous*, *sporophytes* unknown.

**Distribution and ecology.** *Didymodon sibiricus* is currently known from two close localities on Suntar-Khayata Mountain Range in Yakutia, on Byrranga Range in northern Taimyr (this is the northernmost known locality, at 74.47°N), and in several distant localities in southern Siberia: Republics Altai, Tyva, and Buryatia, and Zabaikal-

sky Territory. It was collected on outcrops on dry, open or forested slopes, in cliff niches, on siltstone and dolerite outcrops, at elevations 400–2100 m a.s.l.

**Differentiation.** *Didymodon sibiricus* has a considerable similarity to the described from China *D. daqingi*, and its specimens were previously referred to this species (Ignatova *et al.*, 2024). They are similar in leaf shape, with short, ovate bases and long, linear lanceolate acumina, long excurrent *costa*, and partially bistratose *lamina*. However, they differ in plant size and size of leaves: in *D. sibiricus*, leaves are shorter and narrower [0.8–1.8 (–2.0) $\times$ 0.3–0.4 mm vs 2.0–2.8 $\times$ 0.4–0.5 mm], *costa* is more slender (50–75 vs 75–105  $\mu$ m wide at leaf base), leaf margins are only slightly recurved in midleaf (much stronger recurved to revolute in proximal 1/2–3/4 of leaf in *D. daqingi*; *lamina* cells are smooth in *D. sibiricus* (vs weakly papillose in *D. daqingi*), and it possesses bistratose patches in distal part of leaf not only at margins but also near *costa*, or only in midleaf (leaf *lamina* is described as bistratose only at margins in *D. daqingi*). Another species described from Inner Mongolia, China, *D. manhanensis* C. Feng & J. Kou, has also a certain similarity with *D. daqingi* and *D. sibiricus* in leaf shape,

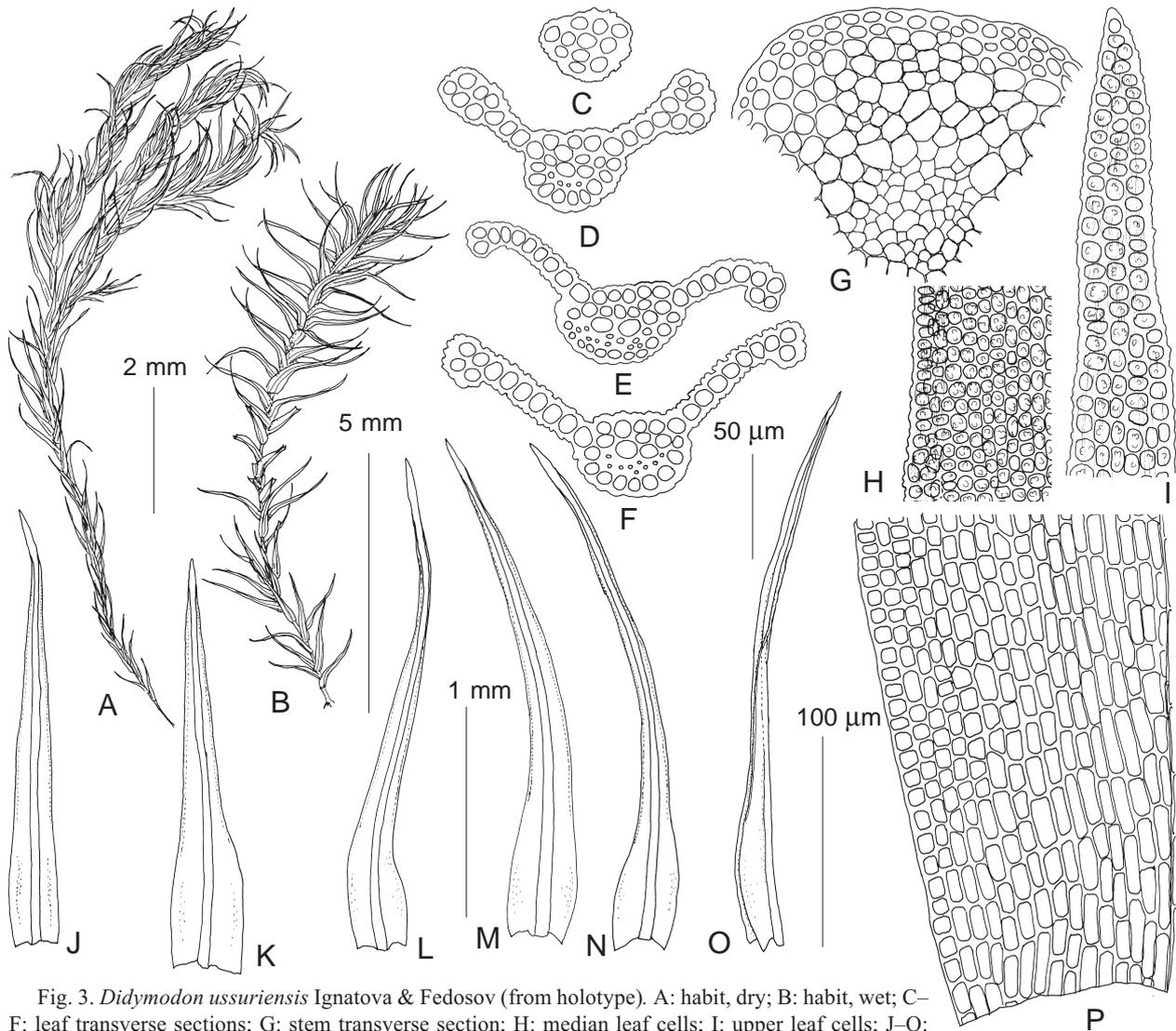


Fig. 3. *Didymodon ussuriensis* Ignatova & Fedosov (from holotype). A: habit, dry; B: habit, wet; C–F: leaf transverse sections; G: stem transverse section; H: median leaf cells; I: upper leaf cells; J–O: leaves; P: basal leaf cells. Scale bars: 5 mm for B; 2 mm for A; 1 mm for J–O; 100  $\mu\text{m}$  for C–I, P.

fragility, and costa structure; its smooth cells provide an additional similarity with *D. sibiricus*. However, its leaves are larger, with wider bases (1.3–2.3 $\times$ 0.43–0.55 mm), leaf margins are stronger recurved, and leaf lamina is bistratose only at margins. Furthermore, it was resolved in an orphaned position in clade 5 of the molecular-phylogenetic tree (Ignatova *et al.*, 2024), far from the clade of *D. sibiricus*.

There are two other species of *Didymodon* in Asian Russia with leaves similar to *D. sibiricus* in shape, having long, linear-lanceolate acumina. One of them, *D. abramovae*, also occurs in the mountains of southern Siberia; it shares with *D. sibiricus*  $\pm$  fragile leaves and long excurrent costa. However, it differs in larger size of leaves (1.5–2.5 $\times$ 0.35–0.5 mm), which are erect when wet (spreading in *D. sibiricus*); its leaf laminae are always unistratose, and its costae possess one layer of guide cells and one layer of ventral stereids. Another species, *D. cherdantsevae*, shares with *D. sibiricus* leaves widely spreading when wet, of similar size (1.7–1.9 $\times$ 0.3–0.35

mm); it differs from it in having unistratose leaf laminae, weakly papillose leaf cells, and costa with one layer of guide cells and one layer of ventral stereids.

*Additional specimens examined*: RUSSIA: **Yakutia**: Oimyakon Distr., valley of Indigirka River, Ust-Nera Settl. surroundings, 6.VIII.2015, *Ignatov & Ignatova 15-1607* (MHA9108746). **Krasnoyarsk Territory**: Taimyr Autonomous District, State Biosphere Reserve Taimyrsky, Ledyanaya Bay, 17.VII.2004, *Fedosov Did1* (MW9035959). **Altai Republic**: Altaisky State Reserve, Karakem River basin, Kobiguayuk Creek, 14.VI.1989, *Ignatov 0/441* (MHA9109024); Karakem River basin, Kukol, 24.VI.1989, *Ignatov s.n.*, Mosses of USSR exs. #19 (MHA 9108720). **Buryatia Republic**: Tunkinskaya valley, Mondy Settl. surrounding, Khulugaisha Mt., *Fedosov 23-0511* (MW). **Zabaikalsky Territory**: Kalar District, Kodar Range, 05.VIII.2012 *Afonina 6612* (LE B-0047639); Kyra District, Sokhondinsky Biosphere Reserve, 08.VII.2010 *Afonina A1010* (LE B-0047631).

***Didymodon ussuriensis*** Ignatova & Fedosov, species nova. Fig. 3.

TYPE: Russia, southern part of Primorsky Territory, Ussurijsky State Reserve, 43.638943°N, 132.556431°E,

ca. 177 m a.s.l., vicinity of Peyshula Field station, Zmeinaya Mt. northern slope. On cliff. 19.VIII.2022, Fedosov 21-02-11 (Holotype MW9131243!, isotype MHA9132130!).

**Diagnosis:** the new species is similar to *Didymodon glaucus* Ryan in plant habit and leaf shape but differs from it in having leaves with 2–3(–4)-layered lamina in 1–4 marginal rows, basal laminal cells weakly differentiated, and in absence of brood bodies.

**Etymology:** the species name refers to the collecting locality of the type specimen, Ussurijsky Reserve and the name of the river Ussuri, which means ‘black as soot’ in Manchu.

**Description.** Plants small to medium-sized, in loose or dense tufts, green or dark-green above, occasionally slightly glaucous, light brownish below, not glossy. Stems 0.7–1.5 cm long, repeatedly branched, with large central strand. Leaves loosely appressed, slightly flexuose when dry in proximal parts of shoots, upper leaves somewhat crisped, widely spreading when wet, 1.7–2.3×0.18–0.32 mm, linear lanceolate to linear, widely keeled distally, with narrow, 2–3 cells wide, 3–4-layered, round in transverse section apical portions 0.1–0.3 mm long, not decurrent at bases; margins plane or weakly recurved in mid-leaf, entire; costa strong, 65–80 µm wide at leaf base, weakly tapering upwards, percurrent, strongly prominent dorsally, flat ventrally, with quadrate cells on both surfaces, papillose on ventral side, without a pad of large, translucent cells below leaf apex, smooth or weakly papillose on dorsal side, semicircular in transverse section, guide cells in 2 layers, 2–5 cells in each layer, dorsal stereid band 1–2-layered, ventral stereid band absent, ventral and dorsal epidermis differentiated; lamina unistratose near costa and in midleaf, with 1–4 rows of 2–3(–4)-stratose cells at margins; cells in distal part of leaves round, short elliptic and oblate, 6–10×µm, with moderately thickened, straight walls, with 1–4 low, bifurcate papillae on both surfaces; basal laminal cells weakly differentiated, chlorophyllose, rectangular, 20–40×9–11 µm, smooth, with moderately thickened walls. KOH reaction yellowish-green or yellow. Brood bodies absent. Dioicous, sporophytes unknown.

**Distribution and ecology.** In addition to the type locality in Ussurijsky Reserve, *Didymodon ussuriensis* was repeatedly collected in Primorsky Territory on Lozovy Range and found once on Russkij Island. It was also revealed in collections from Amur Province (Tukuringra Range in Zeisky Reserve) and from Zabaikalsky Territory (Daursky Reserve). It grows on dry calcareous rocks and outcrops in oak and birch forests; it was also collected on marble blocks on the bank of Zeya reservoir.

**Differentiation.** *Didymodon ussuriensis* is habitually similar to *D. glaucus* in having linear-lanceolate leaves crisped at shoot tips in dry condition, occasionally also with glaucous tint. These two species share a specific structure of leaf tips, 2–3 cells wide, 3–4-layered, round in transverse section. However, *D. ussuriensis* possesses strongly thickened leaf margins, 2–3(–4)-layered in 1–4

rows of cells, flat or weakly recurved at short distance at mid-leaf, whereas in *D. glaucus* leaf margins are always unistratose and recurved. Also *D. ussuriensis* lacks brood bodies (in *D. glaucus* they are frequently numerous), and its basal laminal cells are poorly differentiated, chlorophyllose. The latter character distinguishes it also from *D. australasiae*, which shares with it having 2–3-stratose leaf margins; *D. australasiae* has shorter, lanceolate leaves, costa with a pad of large, translucent cells on ventral surface below leaf apex, and rhizoidal tubers. The latter species is resolved in the molecular-phylogenetic tree (Fig. 1) in the clade representing the genus *Trichostomopsis* sensu Jiménez *et al.* (2022), whereas *Didymodon ussuriensis* is found in the terminal clade of *Didymodon* s.str. There is some resemblance between *D. ussuriensis* and *D. sibiricus* in leaf shape, as they have long and narrow, linear-lanceolate leaves with partially bistratose lamina, costa with guide cells in 2–3 layers, lacking ventral stereids; however, *D. sibiricus* possesses wider leaf bases, 0.3–0.4 mm wide (vs 0.20–0.35 mm wide), leaf laminae with bistratose patches not only at margins, and smooth laminal cells (densely papillose in *D. ussuriensis*).

**Additional specimens examined:** RUSSIA: **Zabaikalsky Territory:** Borzya District, Daursky Reserve, 16.VII.2010 E.S. *Prelovskaya* (LE B-0047621). **Amur Province:** Zeya Reservoir coast between Razvedochny and Sukhoy Gulfs, outcrops, S.V. Dudov & M.N. Kozhin 2016\_Br\_1006 (MW9111441). **Primorsky Territory:** Partizansk District, Lozovy Range, Ignatov, Ignatova & Cherdantseva 06-2814 (MHA9109004); Russkij Island, vicinity of Melkovodnaya Bay, Fedosov 24-351-18 (MW9133389).

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

Species	Isolate	Location	Specimen voucher	ITS	trnG
<i>D. glaucus</i>	OK3491	Russia: Zabaikalsky Territory	Afonina 7411, LE	PV624863	–
<i>D. glaucus</i>	OK3494	Russia: Zabaikalsky Territory	Afonina 7411, LE	PV624864	–
<i>D. glaucus</i>	OK4231	Russia: Irkutsk Province, Slyudyanka	Ignatov & Kazanovsky s.n., MHA9108693	PV624866	PV613702
<i>D. glaucus</i>	OK4232	Russia: Yakutia, Khangalassky District	Ivanova 107005, MW9078137	PV624867	PV613703
<i>D. glaucus</i>	OK4233	Russia: Ingushetia	Bersanova 18-292, MW9091157	PV624868	PV613704
<i>D. glaucus</i>	OK4234	Russia: Perm Territory	Bezgodov 235, MW9090559	PV624869	PV613705
<i>D. glaucus</i>	OK4235	Russia: Buryatia, Baikal Lake	Czernyadjeva 35-14, MW9007680	PV624870	PV613706
<i>D. sibiricus</i>	OK4160	Russia: Altai, Seminsky Range	Ignatov & Ignatova 21-52, MHA9130509	PV624861	PV613700
<i>D. sibiricus</i>	OK4193	Russia: Taimyr, Ledyanaya Bay	Fedosov Did5, MW9035960	PV624860	PV613699
<i>D. ussuriensis</i>	BF200	Russia: Primorsky Territory, Ussurijsky Reserve	Fedosov 21-02-11, MW9131243	PV62487	PV613713
<i>D. ussuriensis</i>	OK4165	Russia: Amurskaya Province, Zeya	Dudov & Kozhin 2016_Br_1006, MW9111441	PV624877	PV613712
<i>D. ussuriensis</i>	OK4210	Russia: Primorsky Territory, Lozovy Range	Malashkina & Ivanov Pr-8-30-13, MHA	PV624879	PV613714