Arctoa (2010) **19**: *51-62*

FIVE SPECIES OF DIDYMODON (POTTIACEAE, BRYOPHYTA) NEW FOR RUSSIA

ПЯТЬ НОВЫХ ДЛЯ РОССИИ ВИДОВ DIDYMODON (POTTIACEAE, BRYOPHYTA)

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Abstract

Didymodon brachyphyllus (Sull.) R.H. Zander, *D. erosodenticulatus* (Müll. Hal.) K. Saito, *D. leskeoides* K.Saito, *D. luridus* Hornsch. and *D. maschalogenus* (Renauld & Cardot) Broth. were discovered as new for Russia during recent floristic investigation of southern Siberia, Russian Far East and Caucasus, as well as a revision on herbarium collections. Two of them, *D. brachyphyllus* and *D. maschalogenus*, were collected in Kamchatka Peninsula, *D. leskeoides* was found in Buryatia and Chukotka, *D. erosodenticulatus* was collected in Altai, Zabaikalskyi and Primorsky Territories, whereas *D. luridus* was revealed in collections from the Black Sea coastal area in Krasnodar Territory. Preliminary key for identification of 29 species of *Didymodon* currently known in Russia is provided.

Резюме

В ходе недавних флористических исследований в Южной Сибири, на Камчатке и Кавказе, а также ревизии гербарных коллекций найдены пять новых для России видов из рода *Didymodon: D. brachyphyllus* (Sull.) R.H. Zander, *D. erosodenticulatus* (Müll. Hal.) K. Saito, *D. leskeoides* K.Saito, *D. luridus* Hornsch. и *D. maschalogenus* (Renauld & Cardot) Broth. Два из них, *D. brachyphyllus* и *D. maschalogenus*, были собраны на Камчатке, *D. leskeoides* найден в Бурятии и на Чукотке, *D. erosodenticulatus* собран на Алтае, в Забайкалье и Приморье, а *D. luridus* выявлен в коллекциях с черноморского побережья Кавказа в Краснодарском крае. Приводится предварительный ключ для определения 29 видов рода, известных в настоящий момент в России.

KEYWORDS: *Didymodon*, floristics, mosses, new records, Pottiaceae, Russia.

Introduction

The knowledge of the genus *Didymodon* in Russia has improved significantly since the publication of the first checklist of the former USSR, where 18 species currently recognized at the species level and 2 varieties were reported (Ignatov & Afonina, 1992). The next checklist (Ignatov, Afonina, Ignatova et al., 2006) included 25 species for the same territory, and 22 of them were from Russia. The number of species in Russia has increased as a result of new records, *D. anserinocapitatus*, *D. gaochienii* and *D. maximus* (Otnyukova, 2002; Afonina, 2004), description of species new for science, *D. hedysariformis* and *D. murrayae* (Otnyukova, 1998, 2002), confirmation of record earlier excluded as dubious, for *D. glaucus* and reconsideration the status of earlier not recognized taxon, for *D. validus* (Kučera,

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unpubl.). Another species, *D. zanderi*, was described a year later (Afonina & Ignatova, 2007). As a result of floristic investigation of the Russian Far East, southern Siberia and Caucasus, accomplished by the first three authors, we were able to add five other species of *Didymodon* to the bryoflora of Russia. We provide descriptions and illustrations of the newly recorded species based on material from Russia, and a key to the identification of 29 species of the genus currently known from the country. It is worth mentioning that the genus is taxonomically difficult, and preliminary results show that additional taxa need to be recognized particularly in *D. validus*/*cordatus*, *D. fallax* and *D. vinealis* species complexes (Kučera, in prep.).

NEW TAXA FOR RUSSIA

Didymodon erosodenticulatus (Müll. Hal.) K. Saito, J. Hattori Bot. Lab. 39: 504. 1975. Fig.1.

Plants small to medium-sized, in dense brownish green tufts. Stems erect or ascending, weakly branching, to 50 mm long, central strand narrow. Leaves appressed and contorted when dry, squarrose-recurved when moist, 2.0-2.7(4)×0.5-0.6 mm, from wide oblong-ovate base gradually tapering into narrowly triangular acumen, keeled in upper part, weakly plicate at base, decurrent; margins irregularly dentate distally, plane or recurved to mid-leaf proximally; costa weak, percurrent or shortly excurrent, with adaxial surface cells linear, smooth, abaxial surface cells subquadrate, smooth or papillose, in transverse section weakly differentiated, in mid-leaf with few guide cells, small dorsal stereid band and ventral and dorsal epidermis of enlarged cells; lamina unistratose, upper lamina cells irregularly rounded-angular or transversely elliptic, thickened at angles, 5-10×5-10 μm, with 1-2 papillae per cell; basal lamina cells enlarged, basal juxtacostal cells irregularly shortly rectangular and quadrate, 15-8×7 μm, thick-walled, smooth or papillose, light brownish-green, basal marginal cells shorter, transversely rectangular, 5×10 μm; cells of decurrences rectangular. [Perichaetial leaves enlargered, widely ovate or ovate-lanceolate, 2.5-3×1 mm, with dentate distal margins]. Sporophytes unknown.

Differentiation. *Didymodon erosodenticulatus* is recognized by dentate distal leaf margins and leaves ovate-triangular, squarrose-recurved when moist. In habit and strongly recurved leaves it is very similar to *D. ferrugineus* (Schimp. ex Besch.) M.O. Hill; moreover, these two species were collected at the same locality and same habitat in Primorsky Territory. However, the latter species differs in totally smooth leaf margins and relatively shorter leaves, ovate in outline. Dentate distal leaf margins differentiate *D. erosodenticulatus* also from *D. giganteus* (Funck) Jur. and D. *maximus* (Syed & Crundw.) M.O. Hill, which share the elongated surface cells on adaxial side of costa.

Comparison of specimens from Russia with Chinese ones reveals some differences: plants from China are larger, with longer leaves and more coarsely dentate margins. However, the diagnostic characters of dentate leaf margins in combination with strongly recurved leaves and elongate adaxial surface cells of costa are present in Russian populations.

Ecology. The species grows usually on wet or dry calcareous rocks, in shaded places. In Altai Mts., it was collected on a rather wet calcareous cliff; in Transbaikalia it grew in a cave on limestone outcrop, in mixed tuft with *Brachythecium buchananii, Cratoneuron filicinum, Plagiomnium* sp.; in Primorsky Territory, the species occupied a similar habitat – dry but shaded limestone outcrop in open oak forest.

Distribution. Japan (Honshu), China, Korea, India (Himalaya), Asiatic Russia.

Specimens examined: RUSSIA: Altai Republic, northern shore of Teletskoe Lake, Izvestkovaya Hill, 51°46'N, 87°33'E, 550 m alt., 12.VI.1989, *Ignatov s.n.* (MHA, MO); Zabaikalsky Territory, 50 km ENE of Nizhnyi Tsasuchey (N of Ust-Borzya settlement), 50°38'N, 115°45'E, *Galanin 4405* (LE); Primorsky Territory, Partizansk Distr., Lozovyi Range, 43°00'N, 133°00'E, 600 m alt., *Ignatov 07-59* (MHA, MW).

Didymodon leskeoides K.Saito, J. Hattori Bot. Lab. 39: 508. 1975. Fig. 2.

Plants in rather dense, reddish-brown tufts, slightly glossy when dry, sometimes with flagelliform attenuate branches. Stems erect or ascending, 1.0-2.0 cm long, often branching, central strand narrow. Leaves oblong-lanceolate, erecto-patent and slightly curved when dry, patent when wet, keeled distally, 0.8-1.6×0.5-0.6 mm, from ovate base gradually tapering into long or rather short narrowly triangular acumen, auriculate at base;

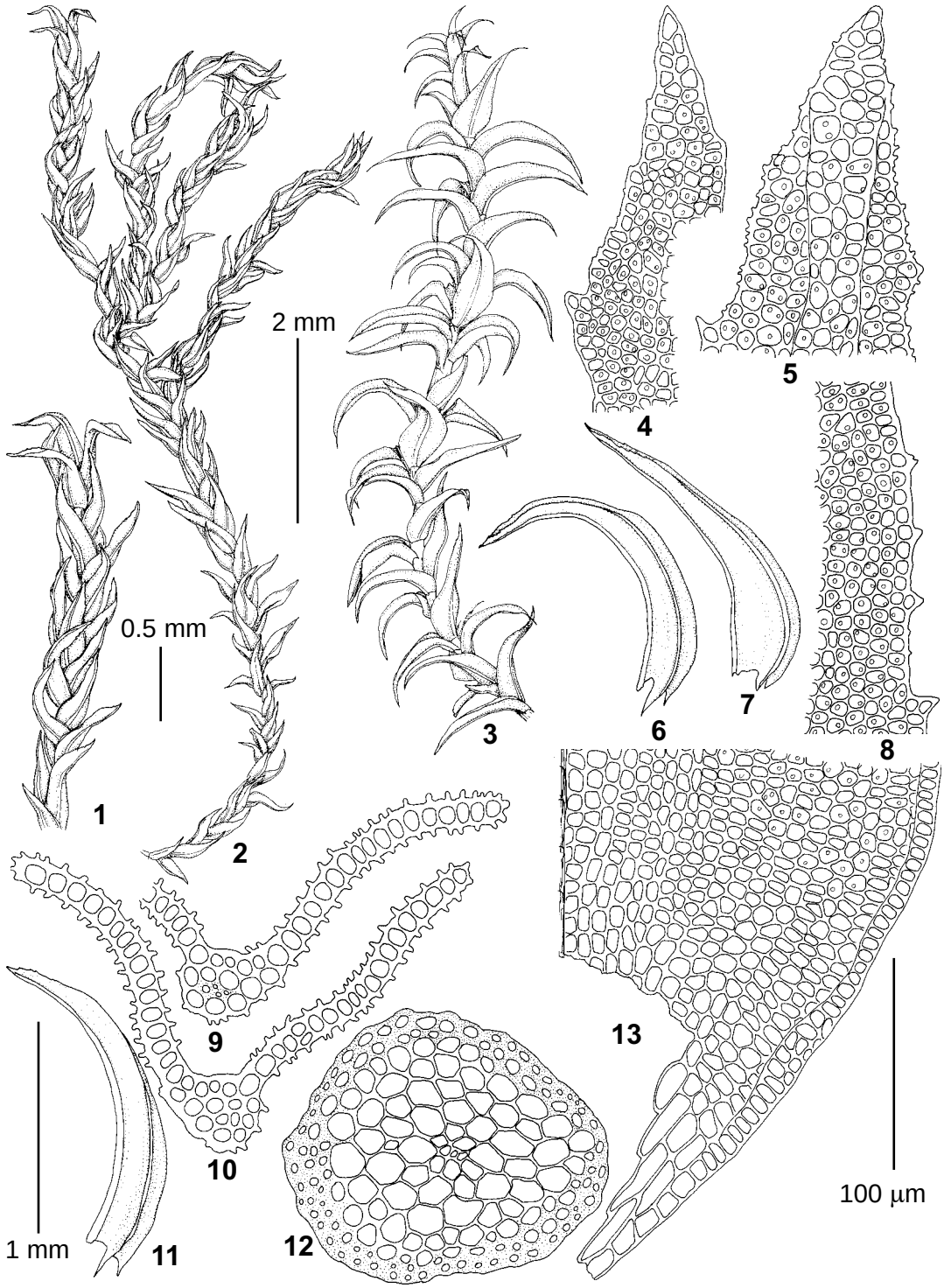

Fig. 1. *Didymodon erosodenticulatus* (from Zabaikal'sky Territory, *Galanin #4405*, LE): 1-2 – habit, dry; 3 – habit, wet; 4-5 – upper lamina cells; 6-7, 11 – leaves; 8 – median lamina cells; 9-10 – leaf transverse sections; 12 – stem transverse section; 13 – basal lamina cells. Scale bars: 2 mm for 2-3; 1 mm for 6-7, 11; 0.5 mm for 1: 100 μm for 4-5, 8-10, 12-13.

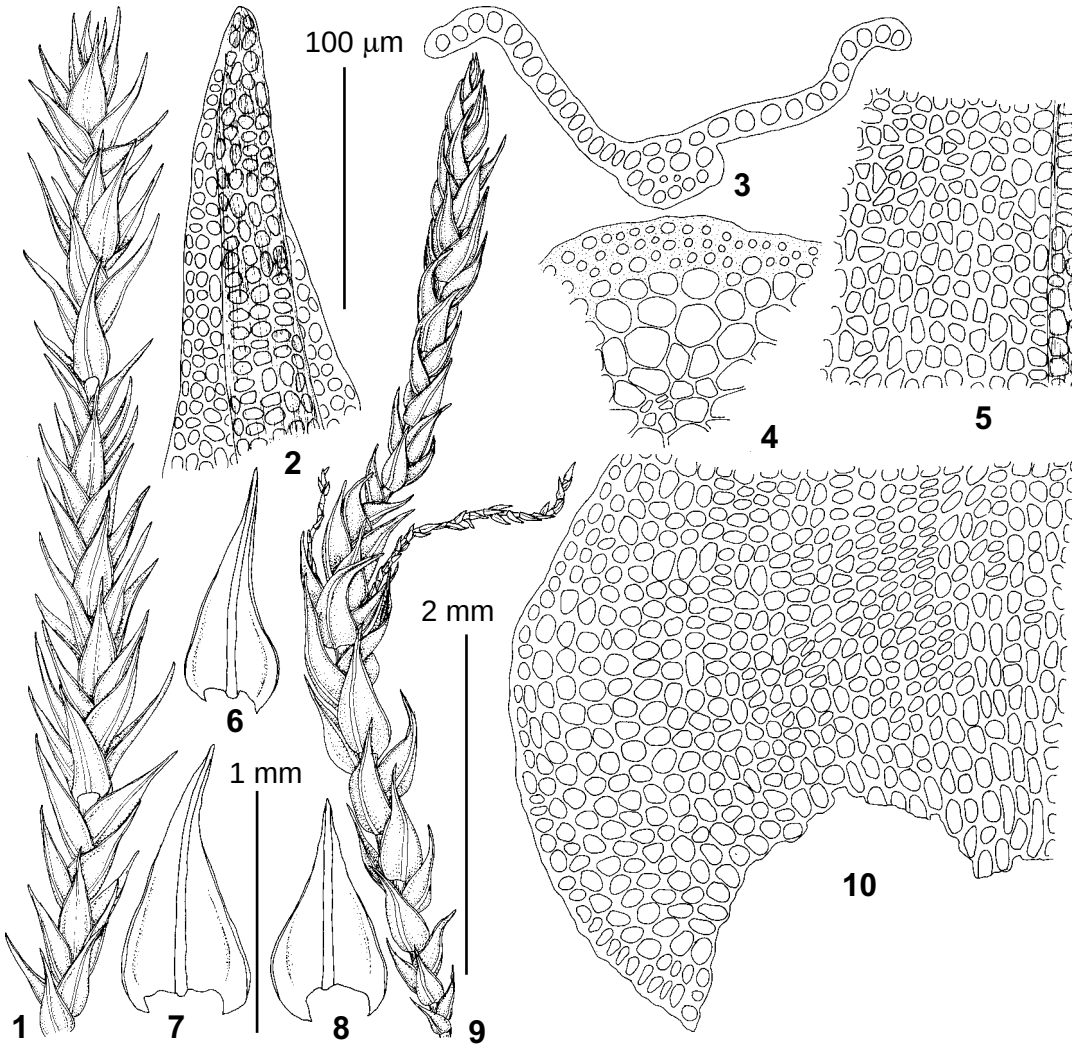

Fig. 2. *Didymodon leskeoides* (from Buryatia, *Afonina #03008*, LE): 1 – habit, wet; 2 – cells of leaf apex; 3 – leaf transverse section; 4 – stem transverse section; 5 – median lamina cells; 6-8 – leaves; 9 – habit, dry; 10 – basal lamina cells. Scale bars: 2 mm for 1, 9; 1 mm for 6-8; 100 μm for 2-5 10.

proximal leaf margins widely recurved to mid-leaf, distal leaf margins plane, unistratose, entire; leaf apex acute, non-fragile; costa strong, gradually narrowing from base to apex, shortly excurrent or percurrent, with adaxial surface cells elongate, thick-walled, slightly sinuose, in transverse section with one row of guide cells, weak dorsal stereid band and ventral and dorsal epidermis; lamina unistratose, upper lamina cells irregular in shape, rounded and oval, 5-8×4-10 μm, thick-walled, smooth, basal cells weakly differentiated, basal juxtacostal cells short-rectangular and quadrate, 13-8×5 μm, thick-walled, basal marginal cells rounded and transverse elliptic, thick-walled, forming auricles 5-12 rows of cells in width. Gametangia and sporophytes unknown. Zander (2007) records the absence of asexual reproduction in North American populations, but he mentions that possibly the species may form axillary gemmae. The plants from Buryatia develop fascicles of fragile axillary shoots with small distant leaves in leaf axils.

Differentiation. Habitus of the plants can vary strongly. Robust plants without flagellae resemble forms of *D. validus*, but differ from the latter in the stem leaves trifarious, glossy, auriculate leaf bases, and elongated cells of the ventral costa surface. Stunted forms may be mistaken for *Didymodon fallax*, which however also lacks auriculate leaf bases.

Ecology. In Buryatia, the species grows on calcareous rocks in larch forest and on steep rocky slopes in *Artemisia commutata* community; it forms rather dense tufts. In Chukotka, it was collected in eutrophic rocky herbaceous tundra with *Dryas*.

Distribution. Asia (northern India, Nepal, China (Yunnan), Russia (see above), Japan (Honshu), North America (Alaska, North-West Territories, British Columbia).

Specimens examined: RUSSIA: Buryatia, Oka Distr., Eastern Sayan Mts., Sorok River valley, 52°34'N, 100°07'E, 1755 m alt., *Afonina 02508, 02608, 03008* (LE); Chukotka Peninsula, Nunligran settlement surroundings, 64°49'N, 175°20'W, 6.VII. 1970, *Afonina s. n.* (LE).

Didymodon brachyphyllus (Sull.) R.H. Zander, Phytologia 41: 24. 1978. — *Barbula brachyphylla* Sull., Expl. Railroad Mississippi Pacific, Descr. Moss. Liverw. 4: 186, pl. 2. 1856. Fig.3.

Plants small, brownish green, often with reddish tones, slightly glossy, in dense or more rarely loose tufts. Stems erect, simple or branching, to 10 mm long, with well-developed central strand. Leaves appressed and incurved when dry, patent when moist, not keeled, 0.5-1.0×0.3-0.5 mm, ovate or ovate-triangular, shortly acuminate, with acute or obtuse apex, often ending in pellucid apiculus of 1-3 cells; leaf margins narrowly recurved from base to apex, unistratose, smooth; costa not or little tapering distally, percurrent or rarely shortly excurrent, strong, 30-50 μm wide at leaf base, surface cells on adaxial side quadrate to short-rectangular, in transverse section with one row of guide cells, dorsal stereid band, ventral stereid band not extending to the apex, ± differentiated dorsal and ventral epidermis; lamina unistratose, distal lamina cells rounded, ovate and rounded-triangular, thick-walled, not sinuous, translucent, 5-8 μm in diameter, with 1-3 papillae per cell, more rarely smooth; basal lamina cells rectangular, with moderately thickened walls, smooth, not porose, alar cells not differentiated. Numerous multicellular axillary gemmae often present, oblong or spherical, yellowish brown or orange, 30-60 μm in diameter. Sporophytes unknown in Russia.

Differentiation. Diagnostic characters of *D. brachyphyllus* include ovate-triangular leaves with margins narrowly recurved from base to apex, subobtuse to widely acute apices, often with short apiculus of 1-3 pellucid cells, and rounded multicellular gemmae in leaf axils. It is closely related to *D. vinealis* (Brid.) R.H. Zander and sometimes is treated as a variety of the latter species (Zander, 1981, 1994). However, in *D. vinealis* the leaves are longer, with apices gradually tapering, not acuminate, leaf margins are commonly bistratose in the upper part. *Didymodon brachyphyllus* is habitually similar to *D. perobtusus* Broth. in small size of plants and occasionally subobtuse leaf apices, but the costa of the former species is thicker, multistratose vs. mostly 3-4-stratose in the latter one, leaf margins are smooth vs. minutely crenulate, many leaf apices are apiculate vs. are always rounded, and axillary gemmae are multicellular vs. unicellular.

Ecology. In Kamchatka, the species was recorded on volcanic lava rocks covered by soil layer and in rock crevices of sea shore cliffs.

Distribution. North America (from Mexico to Alaska, Western Mountain states of U.S.A.), Russian Far East (Kamchatka), Greenland, Iceland, Europe (France, as *D. lamyanus* (Boul.) Thér – see below), Antarctica.

Specimens examined: RUSSIA: Kamchatka, Klyuchevskaya group of volcanoes, NW slope of Ushkovsky volcano, 56°11'N, 160°21'E, 750 m alt., Bilchenok River bank, 21.VII.2003, *Czernyadjeva #53* (LE); 51°46'N, 158°22'E, Pacific Ocean shore, Khodutka Bay, 20.VII.2002, *Czernyadjeva 58* (LE).

Didymodon maschalogenus (Renauld & Cardot) Broth., Nat. Pflanzenf. 1(3): 1192. 1909. — *Barbula maschalogena* Renauld & Cardot, Bull. Soc. Roy. Bot. Belg. 41(1): 53. 1905. Fig.4.

Plants small, yellowish green, slightly glossy, forming loose tufts or growing by separate shoots among other mosses. Stems simple, to 5 mm long, with central strand. Leaves incurved and usually catenulate when dry, patent when moist, weakly keeled distally, 0.6-0.8×0.3-0.4 mm, from ovate base abruptly narrowed into short sharply triangular acumen; margins flat distally, occasionally narrowly recurved proximally, unistratose, smooth; costa strong, percurrent or very shortly excurrent, 40-50 μm wide at leaf base, surface cells on adaxial side elongate-rectangular, in transverse section with one row of guide cells, thin dorsal stereid band, ventral stereid band not extending to distal part of leaf, ventral and dorsal epidermis differentiated; lamina unistratose, distal lamina cells rounded and ovate, thick-walled, 6-8 μm in diameter, often in clear longitudinal rows, bulging on dorsal side, with simple flat papillae or smooth, basal lamina cells short-

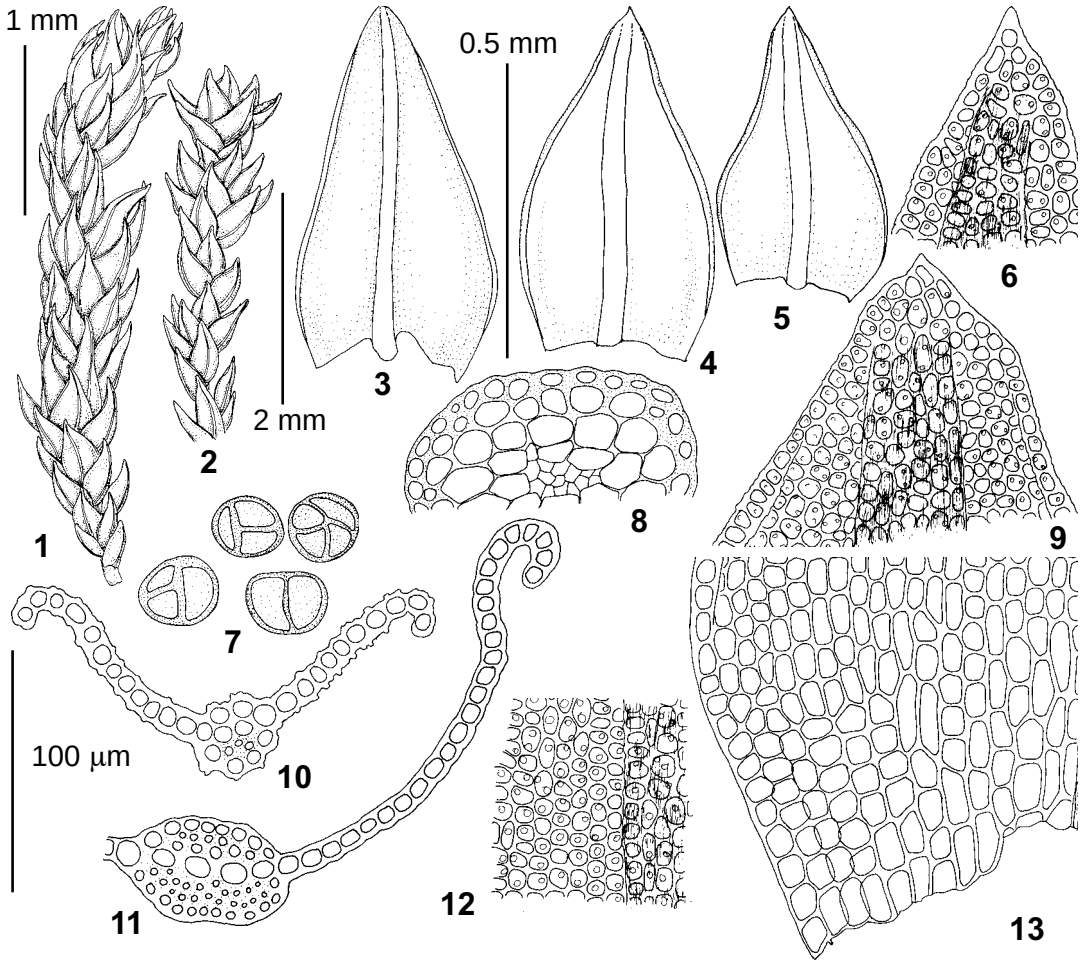

Fig. 3. *Didymodon brachyphyllus* (from Kamchatka, 21.VII.2003, *Czernyadjeva #53*, LE): 1 – habit, dry; 2 – habit, wet; 3-5 – leaves; 6, 9 – upper leaf cells; 7 – gemmae; 8 – stem transverse section; 10-11 – leaf transverse sections; 12 – median lamina cells; 13 – basal lamina cells. Scale bars: 1 mm for 1; 2 mm for 2; 0.5 mm for 3-5; 100 μm for 6-13.

rectangular, with moderately thickened not porose walls, basal marginal cells not differentiated. Numerous spherical or ovate, yellowish-brown or orange multicellular gemmae of 25-30 μm in diameter present in leaf axils. Gametangia absent in plants from Russia. Sporophytes unknown.

Differentiation. Catenulate leaves and elongate cells on adaxial side of costa readily differentiate *D. maschalogenus* from congeners with axillary gemmae like *D. rigidulus* Hedw., *D. cordatus* Jur. and *D. brachyphyllus*.

Ecology. The species was collected on very soft non-calcareous sandstones on rocky slope, in small amount, few shoots with axillary gemmae were intermingled with other mosses.

Distribution. Asia (Iran, northern India, Bhutan, China, Japan, Philippines), North America (Mexico: Chihuahua; U.S.A.: Michigan; Canada: British Columbia, Northwest Territories), Greenland, Europe (Austria, Norway).

Specimen examined: RUSSIA: Kamchatka, Sredinnyj Range, Esso surroundings, ca. 55°56'N, 158°38' E, 750 m alt., Uksichan River bank, 27.VII.2001, *Czernyadjeva #40* (LE).

Didymodon luridus Hornsch. in Spreng., Syst. Veg. 4: 173, 1827. — *Barbula trifaria auct.* Fig. 5.

Plants small to medium-sized, olivaceous green, dark green or brownish, dull, in moderately dense tufts or patches. Stems simple or moderately branching, 3-20 (-30) mm long, with large

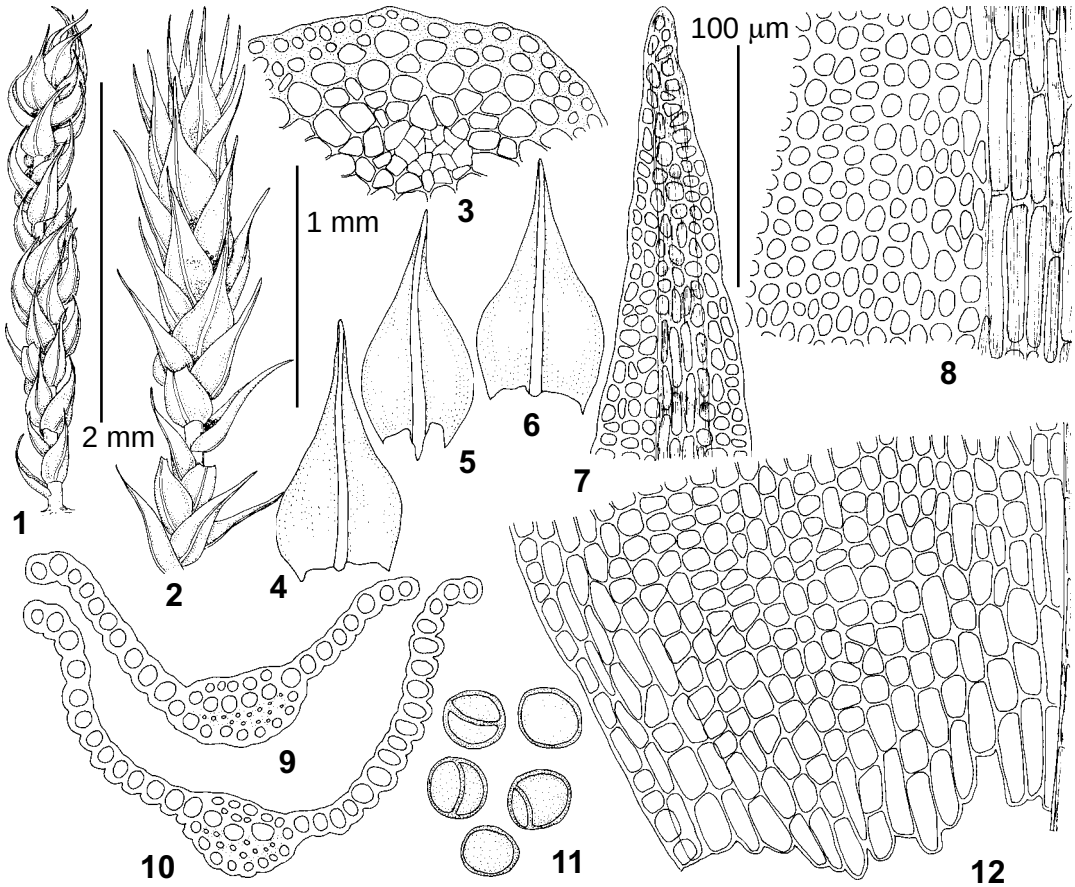

Fig. 4. *Didymodon maschalogenus* (from Kamchatka, 27.VII.2001, *Czernyadjeva #40*, LE): 1 – habit, dry; 2 – habit, wet; 3 – stem transverse section; 4-6 – leaves; 7 – upper leaf cells; 8 – median lamina cells; 9-10 – leaf transverse sections; 11 – gemmae; 12 – basal lamina cells. Scale bars: 2 mm for 1-2; 1 mm for 4-6; 100 μm for 3, 7-12.

central strand. Leaves straight or slightly incurved and appressed, imbricate when dry, patent when moist, widely keeled distally, 0.9-1.5×0.45-0.65 mm, broadly ovate to ovate-lanceolate, obtuse or acute at apex, not or shortly decurrent; margins broadly recurved from near the base to shortly below apex, smooth, unistratose; costa moderately strong, percurrent or ending several cells below apex, gradually narrowing to the apex, 50-75 μm wide at leaf base, surface cells on adaxial side subquadrate or shortly ovate, in transverse section with 1-2 rows of guide cells, dorsal stereid band thick proximally, becoming thin distally, ventral stereid band usually absent, ventral and dorsal epidermal layers differentiated; lamina unistratose throughout, distal and median lamina cells rounded-hexagonal and ovate, thick-walled, 6-10 μm in diameter, smooth, basal lamina cells not differentiated or slightly enlarged and more translucent, short-rectangular, with moderately thickened non-porose walls, 15-20×12 μm, basal marginal cells not differentiated. Sporophytes unknown in Russia.

Differentiation. *Didymodon luridus* was confused with *D. rigidulus* in Russia, with all cited specimens reported earlier as *D. rigidulus* for the projected Utrish Nature Reserve (Ignatova et al., 2005). The leaves are occasionally very similar in shape to leaves of the latter species, being narrowly acute, with percurrent costa, not sharp at the apex. These two species can be separated by unistratose leaf margins in *D. luridus* vs. always bistratose ones in *D. rigidulus*; always smooth and thick-walled lamina cells, hardly differentiated at leaf base vs. often papillose cells, usually differentiated in basal portion near costa, rectangular; axillary gemmae ab-

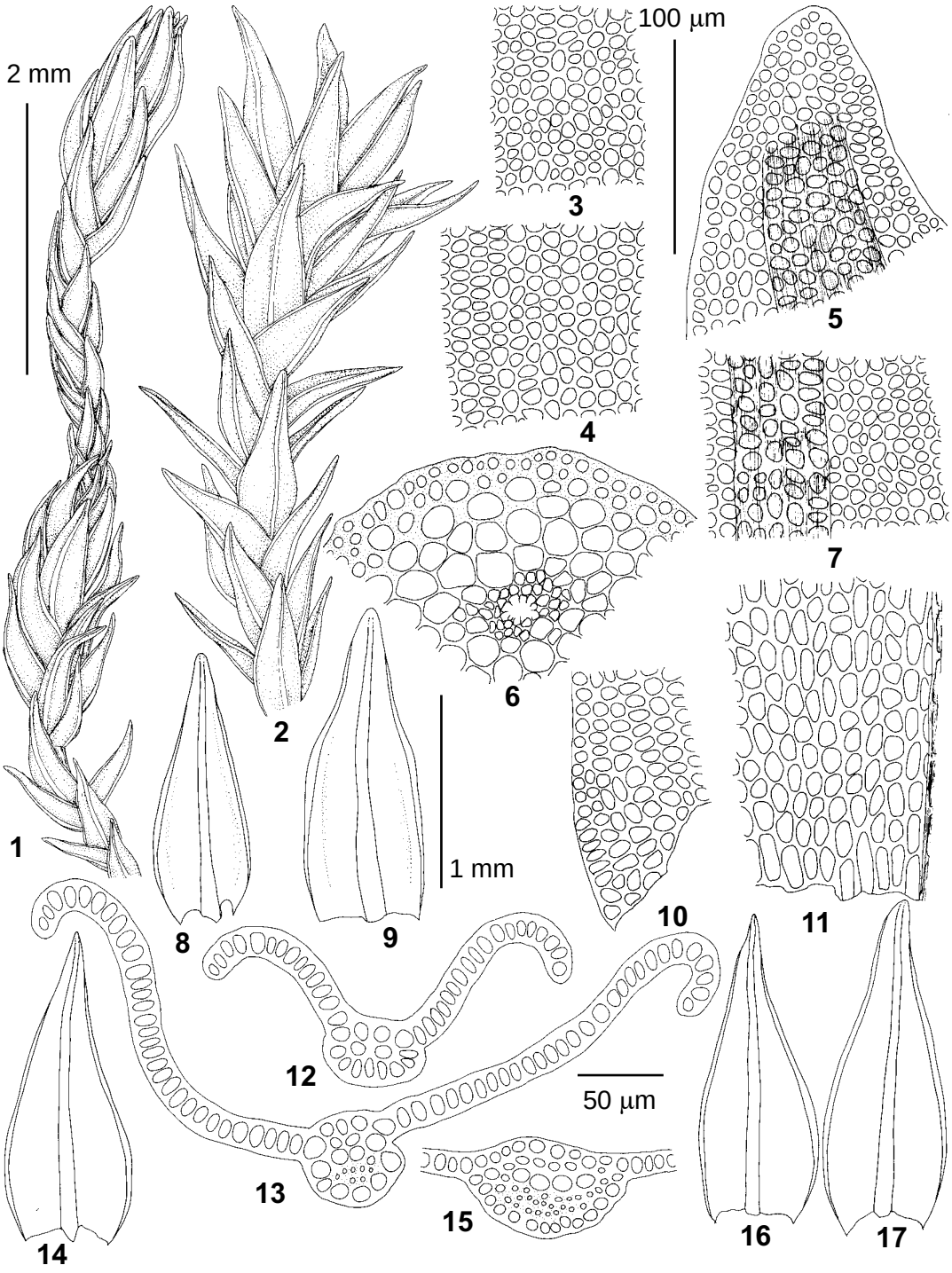

Fig. 5. *Didymodon luridus* (from Krasnodar Territory, Utrish, *Ignatov & Ignatova #05-595*, MW): 1 – habit, dry; 2 – habit, wet; 3 – upper lamina cells; 4 – median lamina cells; 5 – uppermost leaf cells; 6 – stem transverse section; 7 – surface cells of costa on adaxial side; 8-9, 14, 16-17 – leaves; 10 – basal marginal cells; 11 – basal juxtacostal cells; 12-13, 15 – leaf transverse sections. Scale bars: 2 mm for 1-2; 1 mm for 8-9, 14, 16-17; 100 μm for 3-7, 10-11; 50 μm for 12-13, 15.

sent vs. often present. The revision of collections revealed that *D. rigidulus* was not collected in that territory, all its records belong to *D. luridus*. *D. luridus* can be very similar to *D. acutus*, the latter however having narrower leaves with clearly excurrent costa, and perichaetial leaves hardly differentiated versus perichaetial leaves obtuse with costa not reaching the apex. *Didymodon tophaceus*, which may have leaves similar in shape to *D. luridus*, is easily differentiated by elongate adaxial surface cells of costa vs. isodiametric ones in *D. luridus*.

Ecology. The species was collected on rocks and rocky soil on slope to the Black Sea covered by *Pistacia* and *Juniperus* open forest and in stream valleys with *Carpinus orientalis* & *Fagus orientalis* forests.

Distribution. Europe, North Africa, Macaronesia, Western and Central Asia (Turkey, Georgia, Armenia and Azerbaijan, Tajikistan, Kyrgyzstan and Turkmenistan).

Specimens examined: RUSSIA: Krasnodar Territory, Anapa District, between Bol'shoy and Malyi Utrish, *Ignatov & Ignatova 05-478, 05-595, 05-412,* 23.VIII.2004, *Akatova s.n.* (MW); Novorossiysk District, east of Malyi Utrish, Mokraya Shchel', *Ignatov & Ignatova 05-702* (MW); near delphinarium lake, *Ignatov & Ignatova 05-667* (MW).

A PRELIMINARY KEY TO IDENTIFICATION OF *DIDYMODON* SPECIES IN RUSSIA

1. Leaf apices caducous or upper part of lamina strongly fragile 2
— Leaf lamina not fragile, apices not caducous (in *D. icmadophilus*, the uppermost parts of excurrent costa can sometimes be caducous as well) 9
2. Leaf apices differentiated into swollen, thickened propagula consisting entirely of the costa 3
— Leaf apices undifferentiated or differentiated as variously notched and partially fractured units forming a series of caducous segments, including lamina, costa, or both .. 4
3. Propagula with even margins, without constrictions; transverse section of costa with 2 layers of guide cells; upper lamina cells 4-8(-10) µm wide ..... *D. anserinocapitatus*
— Propagula with uneven margins, constricted once or twice medially; transverse section of costa with 1 layer of guide cells; upper lamina cells 8-13(-15) µm wide . *D. johansenii*
4. Leaf apices wide, with lamina of 2-6 rows of cells at each side of the costa, fractured into wide, irregular units 5
— Leaf apices narrow, with lamina of 1-2 rows of cells each, fractured into narrow, square or rectangular units 7
5. Leaves 1.5-4 mm long, crisped when dry, margins at least on young leaves always dentate distally; upper lamina cells mamillose and papillose ..... *D. sinuosus*
— Leaves 0.7-2.0 mm long, not crisped when dry, margins not dentate distally 6
6. Fragile lamina fragments not differentiated into specialized propagula, upper leaf cells mamillose and papillose, 10-14 µm wide .. .. *D. zanderi*
— Lamina fragments differentiated into specialized propagula; upper lamina cells smooth, 6-10 µm wide ..... *D. hedysariformis*

7(4). Fragile apical part of the leaf not segmented, plants robust, dark green, with leaves 1.5-2.5 mm long ..... *D. validus* s.l.
— Fragile apical part of the leaf segmented, plants medium-sized, with brownish tinge, leaves to 1.5 mm long 8
8. Leaf apex straight, regularly notched, forming square or rectangular segments, entire; costa percurrent or ending several cells below the apex; upper lamina cells below the fracture 10-13 µm wide ..... *D. gaochienii*
— Leaf apex straight to flexuose, irregularly notched, forming rectangular segments below, towards the tip indistinctly segmented, the distal segment toothed at tip; costa excurrent; upper lamina cells below the fracture 6-9 µm wide ..... *D. murrayae*

9(1) Leaves linear-lanceolate, usually crisped when dry 10
— Leaves ovate-lanceolate, ovate or deltoid, straight, flexuose or twisted when dry .. 11
10. Plants bluish green, not reacting red in KOH; basal lamina cells strongly differentiated, hyaline, thin-walled; leaf base little expanded; costa usually shortly excurrent, leaf margins mostly narrowly recurved in the upper part of leaf ..... *D. glaucus*
— Plants variously green but commonly with reddish tones in older parts, cell walls react-

ing red with KOH; basal lamina cells not strongly differentiated, not hyaline, with moderately thickened walls; leaf margin mostly plane in the upper part of the leaf, costa not excurrent ..... *D. insulanus*

11. Plants mostly minute, usually dark brown, with leaves (0.3-)0.5-0.9(-1.2)×0.25–0.35 mm, ovate and mostly obtuse, costa weak, mostly not reaching apex, leaf margins crenulate by bulging cell walls 12
— Plants mostly larger, green, brown or reddish brown, with leaves usually longer than 1 mm, apex not obtuse except sometimes in *D. tophaceus* and *D. brachyphyllus*, leaf margin smooth except *D. zanderi* 13
12. Plants with fragile flagelliform innovations; leaves dimorphic, axillary gemmae absent ..... *D. subandreaeoides*
— Plants without fragile flagelliform innovations; leaves monomorphic, axillary gemmae often present ..... *D. perobtusus*
13. Leaf margins minutely crenulate; upper leaf cells mamillose, covered with 2-3 forked papillae ..... *D. zanderi*
— Character combination different 14
14. Leaves markedly auriculate at base, fascicles of fragile flagelliform axillary shoots with small distant leaves sometimes present ..... *D. leskeoides*
— Leaves not auriculate at base, flagelliform shoots absent 15
15. Ventral (adaxial) surface cells of the costa in the upper half of the leaf elongated, not transient from lamina 16
— Ventral (adaxial) surface cells of the costa in the upper half of the leaf ± isodiametric, transient from lamina 23
16. Leaves catenulate when dry; multicellular gemmae usually present in leaf axils ..... *D. maschalogenus*
— Leaves not catenulate when dry; gemmae absent 17
17. Leaves often obtuse at apex or apiculate; costa mostly ending well below apex, rarely percurrent ..... *D. tophaceus*
— Leaves gradually tapering to apex, costa percurrent 18
18. Upper and median lamina cells strongly thick-walled and sinuose, basal lamina cells pitted ..... *D. giganteus*
— Upper and median lamina cells not sinuose, basal lamina cells not or weakly porose ... 19
19. Leaves widely spreading to squarrose when moist, ovate to oblong-ovate, decurrent, sharply keeled; plants sterile, evenly foliated, mostly markedly trifarious; stem cross-section with weak central strand and cortex cells with strongly thickened, dark brown walls 20
— Leaves erectopatent or spreading when moist, ovate-lanceolate, hardly keeled; plants sometimes to commonly fertile, with leaves gradually larger towards apex, not markedly trifarious; stem cross-section with strong central strand and moderately thickened, light brown cortex cells 22
20. Leaf margins dentate in the upper part ..... *D. erosodenticulatus*
— Leaf margins smooth in the upper part . 21
21. Leaves mostly 2.0-2.5 mm long, long ovate, indistinctly trifarious ..... *D. maximus*
— Leaves mostly 1.0-2.0 mm long, ovate, distinctly trifarious ..... *D. ferrugineus*
22. Peristome twisted, > 800 μm long; leaf margins recurved to 2/3-4/5 of the leaf length . ..... *D. fallax*
— Peristome straight, < 550 μm long; leaf margins plane in the upper half . *D. spadiceus*

23(15). Plants robust, rusty brown; stem central strand absent; leaves strongly recurved when moist ..... *D. asperifolius*
— Plants small to robust, green or brownish; stem central strand present; leaves erectopatent to spreading when moist 24
24. Leaves 0.7-1.0 mm long, ovate, widely acute or rounded at apex and often with 1-3-celled pellucid apiculus ..... *D. brachyphyllus*
— Leaves mostly longer than 1 mm, ovate-lanceolate to narrowly lanceolate 25
25. KOH laminal reaction red; ventral stereid band in costa transverse section absent, guide cells in leaves with well-developed costa in 2 rows; papillae dense, sometimes obscuring the lumina ..... *D. vinealis*
— KOH laminal reaction yellowish or orange; ventral stereid band in costa transverse section present except for greatly reduced plants,

guide cells mostly in 1 row; papillae sparse, not obscuring the lumina 26

26. Multicellular axillary gemmae present .. 27
— Axillary gemmae absent 29

27. Distal leaf margins regularly bistratose; leaf apex not sharp; costa not sharply delimited from the lamina in distal part of leaf acumen ..... *D. rigidulus*
— Distal leaf margins unistratose or with few bistratose patches; costa sharply delimited from the lamina in distal part of leaf acumen, excurrent 28

28. Leaves broadly lanceolate to ovate, 1.0-1.8 mm long, with strongly recurved margins and relatively stout costa ..... *D. cordatus*
— Leaves ovate-lanceolate to long lanceolate, up to 4 mm long, margins mostly less markedly recurved ..... *D. validus*

29(26). Distal leaf margins regularly bistratose; leaf apex not sharp; costa not sharply delimited from the lamina in distal part of leaf acumen ..... *D. rigidulus*
— Distal leaf margins unistratose or with few bistratose patches; costa sharply delimited from the lamina in distal part of leaf acumen 30

30. Leaf cross-section rounded in the upper part, lamina cells strongly thick-walled, with rounded lumina, smooth or nearly so; terricolous plants of xero-thermophilous communities ..... *D. acutus*
— Leaf cross-section angular in the upper part, lamina cells less strongly thickened, with rounded-quadrate lumina, papillose or smooth; mostly epilithic plants in a wider variety of regions 31

31 At least some of the leaves with long-excurrent costa (> ca. 20% of the leaf length), lamina cells mostly papillose with papillae merged into longitudinal ridges, costa relatively weak ..... *D. icmadophilus*
— Costa excurrent for less than 15% of the leaf length (except for plants from extreme habitats like deep shade), lamina cells smooth or nearly so, costa commonly relatively strong ..... *D. validus*

Discussion

The growing number of *Didymodon* species known from Northern and Central Asia seems to fill the gaps in knowledge of distribution of the taxa rather than anything else. Species diversity of *Didymodon* in Russia (29 species, 30 with the inclusion of *D. australasiae* known only from other former USSR countries) is now identical to the current known diversity of Europe (27 species included in Hill et al., 2006 need to be amended by the recent records of *D. maschalogenus* and *D. eckeliae*, *D. lamyanus* is considered here to be synonymous to *D. brachyphyllus* but on the other hand *D. validus* is recognized) and only slightly lower than the diversity in North America north of Mexico (Zander, 2007 recognizes 26 species but 5 additional ones would be listed if the species concepts would be identical). The richest regions for *Didymodon* in Russia are in southern Siberia (15 species) and Caucasus (13). It is not surprising, as the genus occurs predominantly in continental regions with cold and dry climate and its species prefer calcareous substrates; such conditions are widely represented in mountains in these areas. Asiatic arctic regions are also rich in species of *Didymodon*: 9 species were recorded for arctic Far East and 8 for arctic Yakutia, while only 5 for arctic East Siberia; 7 species are known from northern part of Russian Far East, 7 for its southern part, and 6 for non-arctic Yakutia (Ignatov, Afonina, Ignatova et al., 2006). The number of species decreases considerably in lowland regions, such as central European Russia, Russian European Arctic and West Siberia. 14 species are known to occur only in the Asiatic part of Russia; however, seven of them are known from Europe. Among the rest seven species four occur also in North America, and only three species, *D. hedysariformis*, *D. gaochienii* and *D. zanderi* are restricted to Asiatic Russia and China.

Of the newly recorded species, the discovery of *D. luridus* in the Russian part of Caucasus was the most expected. The species has a continuous submediterranean and subatlantic distribution, extending to the Central Asian countries of Tajikistan, Kyrgyzstan and Turkmenistan. Its previous records from western North America were not confirmed by Zander (2007). In Russian part of Caucasus, the species was found only locally in the Black Sea coastal area between Anapa and Novorossijsk, with climate and vegetation most similar to Mediterranean.

The record of *D. brachyphyllus* can also be seen as a logical extension of its previously known

distribution area that principally stretches along the Pacific coast from Mexico to Alaska. However, several peculiar disjunctions in the distribution of this species remain, including western Greenland (Mogensen & Zander, 1999), Iceland (Jóhannsson, 2003), Massif Central in European France (cf. Jiménez, 2006), and most interestingly, Antarctica (Zander & Ochyra, 2001).

Didymodon leskeoides, found newly in Buryatia and Chukotka and *D. erosodenticulatus*, recorded in Altai, Buryatia and Primorsky Territory, are both species with relatively little known distribution, which seem to have a relatively contiguous distribution areas, from which however only scattered occurrences are known at present. *Didymodon leskeoides* is known from very scattered records extending from Indian Himalaya over the whole North-Eastern Asia to North America and it might be partly overlooked. Indeed, the specimen from Chukotka was filed under *D. acutus*, similarly as a specimen Schofield 98566 (DUKE) from British Columbia; Saito (1975) also mentions the presence of the species as an admixture, even in a type of another species from Yunnan, China, and similarly comments Sollman (2005). *Didymodon erosodenticulatus* looks distinctive under the microscope but habitually can be easily mistaken for *D. ferrugineus*.

Didymodon maschalogenus has a peculiar distribution area with many unexpected disjunctions but it also may be overlooked. Its distribution centre could be located in the Himalaya, similarly to the preceding two species (Jiménez et al., 2004); the nearest known occurrences are in Japan, China and Canadian Northwest Territories. The species seems to have a preference for disturbed and unstable substrates, as described in detail in Köckinger & van Melick, 2007.

ACKNOWLEDGEMENTS

The work of Afonina and Czernyadjeva was partly supported by RFBR grants #08-04-98021, 10-04-00781, of Ignatova by the Biodiversity Program of Russian Academy of Sciences.

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