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RESEARCH PAPER

On the distribution of *Ditrichum divaricatum* (Ditrichaceae, Bryophyta) in North Pacific region

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ABSTRACT

New data on the distribution of *Ditrichum divaricatum* Mitt. are presented. This species was described from Japan and previously known also from South Korea and China; it is identified in collections from Russia (Transbaikalia, Suntar-Khayata Mt. Range in Yakutia, and the Kamchatka Peninsula) and from Alaska (USA). Most specimens from Russia were previously attributed to *D. pallidum* (Hedwig) Hampe but the revision of the herbarium collections in MW, MHA, and LE did not confirm the presence of the latter species in the country. A description and illustrations of *D. divaricatum* based on Russian specimens are provided as well as data on its ecology; in the north of the Pacific, the species is confined to volcanic substrates of acidic composition.

Keywords: East Asia, bryophytes, Kamchatka, Alaska, rare species, phytogeography

РЕЗЮМЕ

Федосов В.Э., Чернядьева И.В., Афонина О.М., Игнатова Е.А. Новые данные о распространении *Ditrichum divaricatum* (Ditrichaceae, Bryophyta) в Северной Пацифике. Приводятся новые данные о распространении *Ditrichum divaricatum* Mitt. Этот вид был описан из Японии и ранее известен также из Южной Кореи и Китая; он выявлен в коллекциях из России (из Забайкалья, хр. Сунтар-Хаята в Якутии и с п-ова Камчатка) и с Аляски (США). Большинство российских образцов вида было ранее отнесено к *D. pallidum* (Hedwig) Hampe, но ревизия гербарных коллекций в MW, MHA и LE не подтвердила произрастание этого вида в России. Приводятся описание и иллюстрации *D. divaricatum* на основании российского материала и данные о его экологии: на севере Пацифики вид приурочен к вулканогенным субстратам кислого состава.

Ключевые слова: Восточная Азия, мохообразные, Камчатка, Аляска, редкие виды, фитогеография

Recent studies of the moss flora of East Asia revealed numerous cases of erroneous attribution of European names to Asian species (Ignatova et al. 2016, 2019, 2020, Fedosov et al. 2017, 2022a,b). Typically, the reason for such mistakes originates from the historically uneven exploration of different sectors of the Holarctic. Although many historical types originate from Japan, Himalayan region, these species usually remain poorly known or poorly understood by European and Russian scientists. Present paper deals with one of such cases, revealed in the genus *Ditrichum* Hampe.

The checklist of mosses of East Europe and North Asia (Ignatov et al. 2006) included 11 representatives of the genus *Ditrichum*, among which three, *D. cylindricum* (Hedw.) Grout, *D. flexicaule* (Schwägr.) Hampe and *D. gracile* (Mitt.) Kuntze are currently classified in the other genera (Matsui & Iwatsuki 1990, Seppelt et al. 2007, Fedosov et al. 2016, Hodgetts et al. 2020). In course of the ongoing revision of the genus *Ditrichum* in the moss flora of Russia we examined specimens in the largest Russian bryophyte herbaria (IRK, LE, MHA, MW and VGBI) and confirmed that most of these species indeed occur in Russia. Several groups of species appeared in need of a thorough taxonomic revision supplied with molecular phylogenetic study; they will be considered in a separate paper. Also, we failed to confirm presence of *Ditrichum pallidum* (Hedw.) Hampe in Russia. This species was originally described as *Trichostomum pallidum* Hedw. based on Schreber's specimen from Europe and currently is known to occur also in Eastern North America, in few localities in western North America, and East and North Asia (Hodgetts & Lochart 2020). According to Ignatov et al. (2006), this species occurs in Eastern Siberia, Southern Siberia and southern part of the Russian Far East. Actually, these records were based on identifications of Lazarenko (1940) and Bardunov (1969). However, an illustration of a leaf attributed to *D. pallidum* by Bardunov (1969) and his description are remarkably different from those based on European and American specimens (Seppelt et al. 2007, Lüth 2019), so his records, apparently, should be assigned to another species. At the same time, recent lists of mosses of Mus-Khaya Mt. area in Yakutia (Ignatova et al. 2011), Kamchatka Peninsula (Czernyadjeva 2012, Afonina et al. 2022), Transbaikalia (Afonina et al. 2017) and Iturup Island (Bakalin et al. 2019, Cherdantseva et al. 2018) also included *D. pallidum*.

MATERIAL AND METHODS

In the course of the Moss Flora of Russia preparation, we examined specimens referred to *D. pallidum* in IRK, LE, MHA, MW and VGBI using standard anatomic and morphological approach to bryophyte identification (stem, leaf, capsule anatomy and morphology, sexual condition, etc.) and relevant literature referred to in the Results and Discussion sections. Morphological studies and measurements were conducted using

stereomicroscope Nikon SMZ1270 and light microscope Zeiss Axioplan 2 Imagin I Moscow State University or microscopic technique available in the visited herbaria.

RESULTS AND DISCUSSION

We found that no one specimen, referred by Bardunov to *D. pallidum* actually belong to this species. Moreover, specimens from Mus-Khaya Mt. and Kamchatka share two traits unusual for Russian species of the genus: hyaline margins of the leaf lamina composed of several rows of thin-walled cells, and mammillose, serrate leaf subula. These traits make the species easily recognizable and well referable to a Japanese species *D. divaricatum* Mitt., based on descriptions and illustrations of Noguchi (1987) and Matsui & Iwatsuki (1990). Japanese specimens of *D. divaricatum* kept in LE, MHA and MW are identical with Russian specimens from Yakutia and Kamchatka. Although this species has not been reported from Russia by Ignatov et al. (2006), Ignatov et al. (2000) listed not identified species of the genus, which is probably close to *D. divaricatum* or *D. rhynchostegium* Kindb. for the Bureya River upper course based on two specimens collected by Ignatov (07-1221, 07-1222) and three specimens collected by Iwatsuki. Moreover, two specimens from where (Ignatov & Ignatova 07-1221, -07-1223) are represented in the Database of the moss Flora of Russia (Ivanov et al. 2017, accessed 01.07.2023) under the name *D. divaricatum*. We examined these specimens and referred them to the other species. Also we found this species in a single specimen from Transbaikalia and in two specimens from Seward Peninsula, Alaska. Thus, we present a range extension of the species, which is a novelty for the moss floras of Russia and North America, while *D. pallidum* is excluded from the moss flora of Russia.

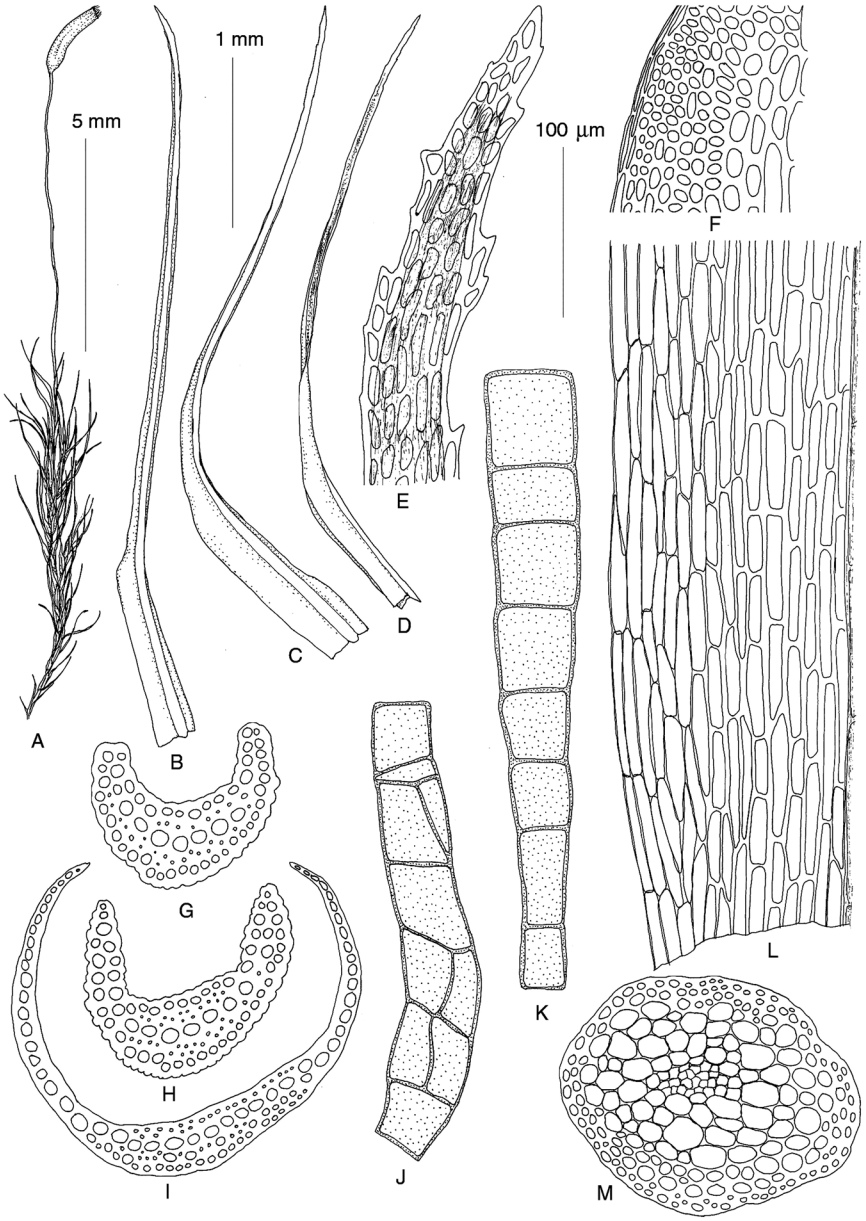

Figure 1 *Ditrichum divaricatum* Mitt. (A–I, L–M – from MW9037012, J–K – from MHA9109533): A: habit, dry; B–D: leaves; E: upper leaf cells; F: cells at leaf shoulder; G–I: leaf transverse sections; J–K: gemmae; L: basal leaf cells; M: stem transverse section. Scale bars: 5 mm for A; 1 mm for B–D; 100 µm for E–M

Ditrichum divaricatum Mitt. Trans. Linn. Soc. London, Bot. 3:155, 1891 (Fig. 1, 2)

Desciption. Plants rather small to medium-sized, largely corresponding *Flexitrichum flexicaule* / *F. gracile* in size and resembling them in habit, typically golden-brown (this species usually grows in exposed environments), yellowish- to brownish green, in loose tufts. Stem 5–10(–14) mm high, simple, with well developed central strand. Leaves 2.5–4×0.3–0.5 mm, from obovate (upper leaves broader at shoulders than at base), semivaginate to tubulose base leaves shouabruptly contracted or, in lower leaves, gradually narrowed to spreading, flexuose, canaliculate, spirally twisted subulae; margins plane throughout or involute at shoulders, entire proximally, crenulate just above leaf shoulders, sometimes sinuose distally; costa greenish, inconspicuously delimited from leaf lamina proximally, brownish in subula, long excurrent, denticulate near leaf tip, in cross-section with two well developed stereid bands separated by arch of guide cells, and dorsal and ventral epidermis, the latter usually developed in distal leaf portion, in several cross sections of subula with distinctly bulging walls; leaf lamina unistratose proximally, bi- to tristratose distally, with very thick outer and inner cell walls and very narrow lumens; upper leaf cells elongate rectangular, 20–35×5–10 µm, thick-walled, just above shoulders 6–17×8–12 µm, irregularly quadrate, rounded to transverse-rectangular, thick-walled; proxi-

mal laminal cells along costa rectangular, 30–55(–76)×8–12 μm, thick-walled, yellowish, becoming narrower and thinner-walled toward margins, along margins in several rows 3–6 μm wide, linear, very thin-walled, hyaline, forming more (in upper leaves) or less delimited limbidium, resembling those found in several species of *Dicranoloma*, transition between thick-walled juxtacostal cells and thin-walled limbidium cells gently V-shaped, so in the basalmost portion of leaf, just above insertion, leaf lamina is composed of thin-walled cells, becoming narrower from costa to margins, the lower row of cells along insertion thicker-walled, fragile, so leaves are easily detachable (like in several species of *Timmia*), but no plants with denudated stem were seen. In few specimens filamentous gemmae-like structures confined to leaf axils occur. Autoicous, perigonia just below perichaetia. Perigonial leaves lanceolate, with short excurrent costa. Perichaetial leaves with very long tubulose base. Setae yellow to brownish, 12–20 mm, straight or slightly flexuose, in transverse section circular, smooth, with central strand. Capsules erect, cylindric, symmetric, rarely slightly asymmetric and inclined, 1.5–2 mm long, brown, darker at transition to seta and at mouth smooth to irregularly rugose. Exothecial cells elongate-rectangular. Peristome with low, ca. 70 μm high, obliquely striolate basal membrane, peach-orange, later whitish teeth, split into two filamentous segments ca. 450 μm long, papillose. Annulus well differentiated, composed of 1–2 rows of large inflated cells. Operculum high conic. Spores papillose, 15–18 μm. *Calyptra cucullate*.

Variation. There are several discrepancies in the descriptions of *D. divaricatum*, provided in the protologue (Mitten 1891), by Noguchi (1987) and Matsui & Iwatsuki (1990) and our description, provided above. First of all, according to the protologue, this species has reddish setae ("theca in pedunculo rubro…"), while according to the Japanese authors and our observations based on Russian specimens, setae are yellowish to brownish. Then, Mitten (1891) provides leaf length measure of 4 mm as characteristic for the species; according to the Japanese authors, it varies from 4 to 6 mm (Matsui & Iwatsuki 1990) or up to 6.5 mm (Noguchi 1987), while our measurements hardly reach 4 mm, even in larger plants. Likewise, the stem length reaches 50 mm according to Noguchi (1987), while our measurements do not exceed 14 mm. Finally, Matsui & Iwatsuki (1990) describe leaf subulae as mammillose (which is indeed a very rare case in Ditrichaceae, even in the broad sense), Noguchi (1987) uses more moderate term "slightly papillose at back", while according to our observations, no clear mamillosity/papillosity can be seen via light microscope in a plain view, but it can be recognized in leaf transverse sections and thus could be better characterized as bulging cell walls, as occurs in *Dicranum septentrionale* Tubanova & Ignatova, *Bucklandiella sudetica* (Funck) Bedn.-Ochyra & Ochyra and *Grimmia anomala* Hampe ex Schimp. One could suggest that north pacific plants considered in the course of present study might represent a different species from that in Japan, where from *D. divaricatum* was described. However, we found no difference between our plants and specimens from Japan edited as exsiccattae of Japanese mosses. In particular, larger Russian plants (LE27-07) exceed Japanese plants (see "specimens examined") in size. Therefore, at the moment we assign our specimens to *D. divaricatum*.

Figure 2 *Ditrichum divaricatum* Mitt. in field conditions (Yakutia, Suntar-Khayatra Range, vicinity of Mus-Khaya Mt. (MHA9109534)

Differentiation. All specimens of *D. divaricatum* were earlier referred to another long-leaved autoicous species, *D. pallidum*; however, hyaline limbidium at proximal part of leaf lamina, as well as occasionally present filiform gemmae differ it from the latter. Due to the combination of long subulate leaves with flexuose denticulate distally subula and differentiated marginal cells in proximal leaf portion, *D. divaricatum* might be confused with *Flexitrichum gracile* (Mitt.) Ignatov & Fedosov. However, in *F. gracile* leaf margins are composed of concolorous, thick-walled cells with oblique lumens, while in *D. divaricatum* they are hyaline, composed of elongate-rectangular to linear, thin-walled cells; juxtacostal cells in basal leaf portion have porose walls in *F. gracile* vs. eporose in *D. divaricatum*; *F. gracile* is characterized by dioicous sexual condition vs. autoicous in *D. divaricatum*; finally, *Flexitrichum* inhabits base rich habitats, while *D. divaricatum* occurs nearly exclusively on acidic rocks. In having combination of hyaline cells at leaf margins and occasionally present mammillose leaf subula *D. divaricatum* resembles rather members of the genus *Distichium* than any other south hemispheric species of *Ditrichum* (Matsui & Iwatsuki 1990). Moreover, autoicous sexual condition differs *D. divaricatum* from most of species of the genus widespread in Northern hemisphere. Also, one of the most helpful traits, allowing recognition of *D. divaricatum* even with stereomicroscope or hand lens is subula spirally twisted along its axis, especially when dry. At the same time, several species with similar combination of traits occur in Southern hemisphere. For example, *Ditrichum ditrichoideum* (Cardot) Ochyra and *D. cylindricarpum* (Müll. Hal.) F. Muell. have mammillose leaf subulae and hyaline or at least differentiated cells at leaf margins; *D. conicum* (Mont.) Mitt., *D. hyalinocuspidatum* Cardot, and *D. hyalinum* (Mitt.) Kuntze share differentiated, in several species hyaline cells at leaf margins; geographical origin of specimen distinguish *D. divaricatum* from all Southern hemispheric species of the genus. Moreover, presence of filiform gemmae is not characteristic for southern hemispheric taxa, among which only *D. gemmiferum* Ochyra & R.I.L. Sm. (closely related to *D. ditrichoideum*) has gemmae, although not filiform. Wide spreading in wet conditions leaves and strongly mammillose leaf subulae differ two later species from *D. divaricatum*. *Ditrichum strictum* (Hook. f. & Wilson) Hampe differs from *D. divaricatum* in having sinuose cell walls in lower leaf portion, lack of limbidium and reduced peristome. *Ditrichum conicum*, *D. hyalinum* and *D. hyalinocuspidatum* Cardot are smaller, short-leaved species (see Seppelt 1982, Ochyra et al. 2008) with leaf subulae hardly reaching the lower portions of their leaves in length. Finally, *D. cylindricarpum* differs from *D. divaricatum* in having less differentiated limbidium, reddish setae and long cylindric capsules, reaching 5 mm.

Ecology and distribution. *Ditrichum divaricatum* was described from Japan (see Matsui & Iwatsuki, 1990 for details of the species lectotypification) and mostly occurs in Pacific region in the areas where volcanogenic rocks occur. It is widespread throughout Japan, known from a single collection in Korea (Matsui & Iwatsuki 1990), and was revealed

in at least five localities in Kamchatka Peninsula and one locality in Western Alaska. On the other hand, *D. divaricatum* is known from scattered isolated localities in continental Asia, in the Stanovoe Upland near Aku Volcano in northern Transbaikalia and near the highest peak of Suntar-Khayata Mt. range (Mus-Khaya Mt.) in Yakutia. The environments of the latter area are described in details by Ignatova et al. (2011); it is characterized by harsh continental climatic conditions and extensive outcrops of ferriferous rocks. Also, in the online database of Consortium of North American Bryophyte Herbaria (https://bryophyteportal.org/portal/collections/list.php, accessed 20.06.2023) two specimens from the Nanchuan, Mt., Sichuan, China are listed, and counting newly revealed localities of the species in North Asia, its presence in this region seems possible. At the same time, no collections from Kuril Islands, which were extensively studied for bryophytes during last decades, were revealed; the species can also occur in volcanic islands of Aleutian Arch, but was never recorded from there in publications and databases of world herbaria. Absence of the species on small Islands with high volcanic activity might be caused by extinction due to eruption events. The distribution in few areas remarkably distant from each other might indicate a relic nature of the species, but also can reflect poor and uneven exploration of the moss flora of North Asia.

According to Matsui & Iwatsuki (1990) and our data, *Ditrichum divaricatum* mostly occurs in the alpine belt on acidic rocks: in rock crevices on lava fields, on boulders with a layer of soil, in rocky dwarf-shrub lichen tundra and in lichen-moss dominated *Pinus pumila* thickets, mostly associated with other pioneer mosses like *Oligotrichum falcatum* Steere or liverworts such as *Diplophyllum*.

Specimens examined

RUSSIA: Trans-Baikal Territory: Kalarskiy District. Stanovoye Nagor'e Uplands, the main plateau, near the Aku Volcano, tundra belt, *Rhododendron aureum* – *Cassiope* sp. – *Carex* sp. – lichen dominated community, on rocks, 56°09'23.1"N 117°30'05.3"E, 2088 m alt., 22 VIII 2014, Mamontov 502/1 (LE). **Republic of Sakha (Yakutia):** Suntar-Khayata Range, Mus-Khaya Mt., Knoriy Creek, 62°33'N 140°56'E, 1770 m alt., rock field, 17 VII 2011, Ivanov (MW9037008, MHA9109534); the same place and date, Ignatov & Ivanov 11-3545 (MW9037010, MHA9109536); the same area, 62°34'N 141°03.5'E, 1680 m alt., dry dwarf-shrub – lichen dominated tundra, 14 VII 2011, Ignatov & Ignatova 11-3225 (MW9037009, MHA9109535), the same place and date, 1700 m alt, dry rocky tundra, Ignatov & Ignatova 11-3227 (MHA9109537). **Kamchatka Territory:** Sredinny Range, Esso Settl. vicinity, stream Uboynyy, 55°60'N 158°41'E, ca 1000 m alt., on stones with a layer of soil on lava fields, 1 VIII 2001, Czernyadjeva 54 (LE); the same area, 55°57'N 158°39'E, 1050 m alt., on soil in dwarf-shrub lichen tundra, 4 VIII 2003. Czernyadjeva 83 (LE); the same area, middle course of the Irakan river, 55°49'N 158°46'E, 1070 m alt., in stone crevices on stony-gravelly area, 9 VIII 2003, Czernyadjeva 88 (LE); the same place, on soil in stony dwarf-shrub lichen tundra, 10 VIII 2003, Czernyadjeva 90 (LE, MHA9109533); the same place, in stone crevices in stony dwarf-shrub lichen tundra, 11 VIII 2003, Czernyadjeva 92 (LE); the same area, road to Gorgochan pass, 55°55'N 158°42'E, 680 m alt., in stone crevices on stony screes, 18 VIII 2003, Czernyadjeva 102 (LE). SE slope of Ichinsky volcano, vicinity of Arbunat Lake, 55°32'N 157°37'E, ~800 m alt., on stones with a layer of soil on lava fields, 3 VIII 2007, Czernyadjeva 4-07 (LE); the same place, on stones with a layer of soil in lichen-moss *Pinus pumila* thickets, 4 VIII 2007, Czernyadjeva 6-07 (LE); the same place, in stone crevices in dwarf-shrub lichen tundra, 4 VIII 2007, Czernyadjeva 7-07, (LE); the same place, in rocks crevices on lava fields, 13 VIII 2007, Czernyadjeva 27-07 (LE); Kostina Mt. western slope, 55°10'N 158°07'E, ~1300 m alt., mountain tundra, on bare patch of soil, 5 IX 2010. Fedosov (MW9117952). Klyuchevskaya group of volcanoes: northwestern slope of Ushkovsky volcano, 56°11'N 160°21'E, ca 1300 m alt., on stones with a layer on lava fields, 16 VII 2003, Czernyadjeva 18 (LE); western slope of Ushkovsky volcano, 55°58'N 160°16'E, 1290 m alt., in stone crevices on lava fields, 19 VIII 2004, Czernyadjeva 85 (LE); western slope of Ushkovsky volcano, 55°58'N 160°15'E, 1450 m alt., on stone in dwarf-shrub tundra, 21 VIII 2004, Czernyadjeva (LE). Kronotsky State Reserve, Krasheninnikov Volcano caldera, 54°35'42"N 160°13'44"E, ca 800 m alt., moist shaded cliff niche, on finesoil, 11 IX 2012, Fedosov 12-346, 12-348 (MW9037011, MW9037014), 12-123 (MHA9109532); the same area, Krasheninnikova Volcano slope, 54°36'12"N 160°16'26"E, ca 1500 m alt., in montane tundra, 10 IX 2012, Fedosov 12-364, 12-178 (MW9037012, MW9037013).

JAPAN: Honshu: Gifu Prefecture, Mt Ontake near Nigorigo, ca. 1900 m alt., on soil-covered rocks by a stream, 18 X 1962, Iwatsuki (Musci Japonici ser. 19, #913, LE); Yamanashi-ken, north slope of Mt. Fuji, ca. 2400 m alt., on rocks covered with soil, 25 VIII 1978, T. & K. Osada (Musci Japonici Exsiccati ser. 32, #1566, LE).

U.S.A.: Alaska: Seward Peninsula, Lost Jim Lava Flow, in deep crevices, 65°33'N 163°52'05W, 122–183 m alt., 13 VII 1992, Afonina Lev-1 (ALA, LE).

Affinities. As was considered in the "Differentiation" section, all morphologically similar to *D. divaricatum* species of the genus *Ditrichum* occur in Southern Hemisphere, mostly in subantarctic region. Moreover, Matsui & Iwatsuki (1990) considered one of south hemispheric species, *D. cylindricarpum*, as its closest relative; they also mentioned similarity of *D. divaricatum* to *Distichium* due to mammillose leaf subulae and vaginate leaves. Interestingly, in 19th and early 20th centuries several south hemispheric *Ditrichum* species were classified in the genus *Pseudodistichium*. Thus, although Fedosov et al. (2016) excluded phylogenetically discordant *Flexitrichum* from the genus *Ditrichum*, structural diversity within the genus *Ditrichum* s.str., as well as its polyphyly (see Fedosov et al. 2016, Bonfim Santos et al. 2021) show need in thorough taxonomic revision of the genus. In particular, further molecular phylogenetic studies are needed to clarify relationships between *D. divaricatum* and south hemispheric species of the genus and estimate their affinities in phylogenetic context.

Brief comment on the exclusion of *Ditrichum pallidum* from the Russian moss flora. *Ditrichum pallidum* was described from Central Europe and is known to occur in Azores, Central and Western Europe with few localities in southern shore of Britain, Sweden and in NW Turkey, thus, avoiding both Northern Europe and Mediterranean region; also it is widespread in Eastern North America, generally southwards Canadian border; records from East and South-East Asia may need in reexamination. Anyway, with such distribution, *D. pallidum* can be considered as a thermophilous species, confined to rather humid environments; its presence is Russia seems possible in the southern part Black Sea coastal area and in western Caucasus, where many other European mosses, occurring in temperate climate (*Buxbaumia viridis* (Moug. ex DC.) Brid. ex Moug. & Nestl., *Cryphaea heteromalla* (Hedw.) Brid., *Hookeria lucens* (Hedw.) Sm., *Nogopterium gracile* (Hedw.) Crosby & W.R. Buck, *Orthotrichum tenellum* Bruch ex Brid., *Pulvigera lyellii* (Hook. & Taylor) Plášek, Sawicki & Ochyra, *Ulota crispa* (Hedw.) Brid., *U. coarctata* (P. Beauv.) Hammar) penetrate.

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