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ON THE GENUS *TORTELLA* (POTTIACEAE, BRYOPHYTA) IN RUSSIAN ARCTIC

О РОДЕ *TORTELLA* (POTTIACEAE, BRYOPHYTA) В РОССИЙСКОЙ АРКТИКЕ

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Abstract

Herbarium collections of *Tortella* and *Trichostomum* from the Russian Arctic in LE, MW and MHA were revised according to the emended understanding of species volume in recent literature. *Tortella splendida* was found to be the most frequent in this territory and *T. spitzbergensis* appeared to be common in northern Taimyr and Chukotka, while distribution of *T. tortuosa* in the Russian Arctic is likely restricted to Chukotka and Polar Urals. *Tortella cuspidatissima* is newly recorded to Chukotka, in addition to the single known locality in the lower course of Lena River. The relationships between Scandinavian and Chukotkan specimens of this species based on molecular markers and morphological characters are discussed. *Tortella fleischeri* is found for the first time in European Arctic, as well as in Russia; its presence here is confirmed with molecular barcoding.

Резюме

Гербарные коллекции *Tortella* и *Trichostomum* из российской Арктики в гербариях Санкт-Петербурга и Москвы (LE, MW и MHA) были изучены и отчасти переопределены согласно новому пониманию объема видов в недавно опубликованных работах. *Tortella splendida* оказалась наиболее частым видом рода на этой территории, *T. spitzbergensis* также нередко встречается на севере Таймыра и Чукотке, в то время как распространение *T. tortuosa* в российской Арктике ограничено Чукоткой и Полярным Уралом. *Tortella cuspidatissima* впервые приведена для Чукотки, в дополнение к единственному известному в России местонахождению этого вида в низовьях р. Лена. Обсуждаются сходство и отличия между образцами этого вида из Скандинавии и с Чукотки, выявленные с помощью молекулярных маркеров и изучения морфологических признаков. *Tortella fleischeri* впервые приведена для европейской Арктики и для России в целом; присутствие этого вида в данном регионе подтверждено с помощью молекулярного баркодинга.

KEYWORDS: mosses, herbarium collections, Arctic, molecular barcoding

INTRODUCTION

A number of expeditions have been conducted in the vast and inaccessible territory of the Russian Arctic since the end of the 19th and especially in the 20th century. Study of vegetation and flora of this region resulted in accumulation of extensive herbarium collections, including mosses. The history of bryological exploration of the Russian Arctic was overviewed in detail by Afonina & Czernyadjeva (1995), who provided the list of 530 moss species occurring in this territory. Their distribution was listed according to 15 subdivisions of the Russian Arctic which were suggested by Yurtsev *et al.* (1978). This list included 4 species of *Tortella* (Lindb.) Limpr. and 2 species of *Trichostomum* Bruch, namely *Tortella arctica* (H. Arnell) Crundw. & Nyholm (in 7 regions of 15), *T. fragilis* (Hook. & Wilson) Limpr. (12 regions), *T. inclinata* (Hedw. f.) Limpr. (based on one literature record from Yana-Kolyma region of Yakutia: Abramova & Stepanova, 1986), *T. tortuosa* (Hedw.) Limpr. (13 regions), *Trichostomum arcticum* (7 regions), and *T. crispulum* Bruch (2 regions). One more species, *T. alpicola* Dixon, was reported by Otnyukova *et al*. (2004) from Northern Taimyr and Chukotka. Later on, Werner *et al*. (2014) published the results of their molecular-taxonomic study of *Tortella artica* and *Trichostomum arcticum* complex. They suggested to recognize 3 species of this complex within *Tortella*: *Tortella arctica*, *T. spitzbergensis* and *T.* ×*cuspidatissima* (presumably a hybrid between *T. arctica* and *T. spitzbergensis*). The distinctions between these 3 species were discussed, key to their identification was provided and their distribution was overviewed. Werner *et al*. (2014) considered *T. arctica* to be widespread

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throughout North American and Eurasian Arctic regions, whereas they could confirm the presence of *T. spitzbergensis* in Canada (Newfoundland), Spitsbergen and Russia (Chukotka, North and South Siberia) and of *T. cuspidatissima* only in its type locality in Alaska and in Sweden. Several specimens of *T. arctica* and *T. spizbergensis* from Russia were also included in the molecular-phylogenetic analyzis provided by these authors; they were listed and supplemented by GenBank accession numbers. Subsequently, Köckinger & Hedenäs (2023), in the course of their study of *Tortella tortuosa*-complex in Europe, found in the Austrian Alps plants which were very similar in morphology to the arctic species *T. arctica*, except for the frequent presence of two layers of guide cells in transverse section of costa close to leaf base. The latter species was described from Russia, Kumachsur in the lower course of Lena River based on collection of H. Nilsson-Ehle; its holotype (in UPS) and isotype (in S) specimens were re-studied by Hedenäs, and it became clear that these specimens are morphologically identical to the plants which were treated as *T.* ×*cuspidatissima* by Werner *et al*. (2014). Thus, the name *Tortella arctica* could not be applied to the widespread arctic species, as well to the plants from the Alps. Then *Tortella splendida* Köckinger & Hedenäs was described in 2023 from the Austrian Alps; these authors mentioned that it is frequent in the Austrian Alps, found in Switzerland, but obviously absent in Northern Europe; they also tentatively supposed that this name could be applied to the plants from non-European Arctic, but it requires more careful study.

Since the treatment of the genus *Tortella* was needed for the next volume of the "Moss Flora of Russia", but distribution of some its species remained vague, the revision of its collections, in particular from the Russian Arctic, was desirable. This is the subject of the present study. We also applied molecular barcoding to confirm the identity of a restricted number of recently collected specimens, both from Arctic and montane areas situated southwards which were suitable for DNA amplification, since the majority of herbarium collections from the Russian Arctic are too old for this purpose.

MATERIAL AND METHODS

Herbarium collections from the Russian Arctic in LE (most extensive), MW and MHA stored under the names *Tortella arctica*, *T. tortuosa*, *Trichostomum arcticum* and *T. cuspidatissimum* Cardot & Thér. were revisited and identified, taking into account the treatments by Werner *et al*. (2014) and Köckinger & Hedenäs (2023). The traditional morphological methods were applied in this study. In addition, 13 specimens were selected for molecular study.

Phylogenetic part of study was based on the nuclear ITS region. 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). Newly obtained sequences were complemented by GenBank data obtained mainly by Werner *et al.* (2014) and Köckinger & Hedenäs (2023), and six accessions of *Tortella squarrosa* (Brid.) Lindb., *T. humilis* (Hedw.) Jenn. and *T. alpicola* Dixon were added for rooting the tree. So, the final ITS dataset included 62 terminals. Voucher data of the originally studied specimens and GenBank accession numbers for the newly generated ITS sequences are provided in Table 1; Genbank accession numbers of sequences downloaded from GenBank are reflected in the tree. Dataset was aligned manually using BioEdit (Hall, 1999). Indel data were scored for using the simple indel coding (SIC) approach (Simmons & Ochoterena, 2000) in SeqState 1.4.1. (Müller, 2005) and added to the datasets prepared for phylogenetic analyses. Bayesian analysis in MrBayes 3.2.7. (Ronquist *et al*., 2012) were set for 5 million generations and sampling frequency one tree each 1000 generations, average standard deviations of split frequencies were checked to have decreased below 0.01 after first 1 million 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, GTR+G+I model of nucleotide substitutions and otherwise standard settings.

RESULTS

Morphological study

Here we do not consider two species occurring in the Russian Arctic: *Tortella fragilis,* which is not rare in Arctic and usually easily identified, and *T. alpicola,* known only from the localities already listed by Otnyukova *et al*. (2004). These species, however, are included into the key to identification of the Arctic species of *Tortella*.

Tortella splendida. We apply here this name to the plants from the Russian Arctic (see discussion below). This species is the commonest in the region, occurring both in its continental part and on islands of the Arctic ocean. Its presence in all regions listed by Afonina & Czernyadjeva (1995) is confirmed by herbarium specimens except for Anabar-Olenek Region (herbarium specimens in SASY should be also checked).

Selected specimens examined: **Nenetz Autonomous District**: Barents Sea, Matveev Island, dwarf shrub-sedge-moss tundra, 69°28'25.7"N, 58°30'9.7"E, 27.VIII.2020, *S.V. Sidorenko & Czernyadjeva* (LE B-0040282). **Arkhangelsk Province: *Novaya Zemlya Archipelago***: South Island, Malyye Karmakuly Settlement, 72°23'N, 52°44'E, 7.VII.1904, *R.R. Pole* (LE). **Krasnoyarsk Territory, Taimyrsky Dolgano-Nenetsky District: *Severnaya Zemlya Archipelago***: October Revolution Island, Zhiloy Peninsula, grass-herb-moss-lichen spotty tundra, ~79°28'N, 94°03'E, 7.VIII.2000, *I.N. Safronova 45* (LE);

same island, Gremyachya River, 8.VII.1985, *M. Gavrilo 8* (LE); Bolshevik Island, p/st Solnechnaya, herb-moss-lichen community, 78°13’N, 103°15’E, VIII.1997, *N.N. Matveeva 11* (LE); same island, Studenaya River, herb-*Poa*-moss community, 78°37’N, 101°05’E, 14.VIII.1998, *N.N. Matveeva 66* (LE). ***Kara Sea***: Archipelago of islands of Izvestij TSIK, Troynoy Island, Kruglaya Bay, 75°57’24"N, 82°34’29"E, 35 m a.s.l., polygonal gravelly grass-moss tundra, 4.IX.2021, *Czernyadjeva 9-21* (LE B-0043056); Nordenskiöld Archipelago, Bianka Island, Cape Povorotnyy, 76°44’54"N, 97°14’07"E, herb-moss community, 6.IX.2023, *Czernyadjeva 30-23* (LE); same archipelago, Tyrtov Island, Cape Povorotnyy, ~76°39’N, 97°28’E, herb community, 9.VIII.1948, *B.N. Gorodkov 12* (LE); same archipelago, Russkyy Island, ~77°02’N, 95°58’E, 15.VIII.1993, *M.V. Melnikov* (LE); Sergei Kirov Islands, Slozhnyy Island, 77°05’03"N, 88°51’01"E, lichen-moss community, 1.IX.2023, *Czernyadjeva 4-23* (LE); same archipelago, Isachenko Island, Ugol’naya Bay, 77°11’09"N, 89°31’40"E, *Juncus*-moss community, 2.IX.2023, *Czernyadjeva 13-23* (LE); ***Taimyr Peninsula***: Cape Chelyuskin, 77°43’N, 104°18’E, 7.VIII.1981, *Makhonin* (LE); Mamontovaya River, sedge-moss tundra, 75°17’N, 95°23’E, 19.VIII.1949, *B.A. Tikhomirov & G.N. Uvarov* (LE); Syrutaturku Lake, 73°35’N, 97°30’E, eutrophic mossy tundra, VIII.1994, *E.B. Pospelova* (MW9068453); Byrranga Range, right bank of Bolsjaya Bootankaga River, forb-sedge spotty tundra, 8.VII.1991, *V.B. Kuvaev 1752* (MW9068454); Bikada Creek, tundra, on hillock top, 10.VIII.1978, *M. Sokolova* (MW9076999); Dikson Area, 73.543°N, 80.658°E, lower slope of hill northward Dikson village, rich fen, 07.VIII.2019, *Fedosov & D. Koltysheva* (MW9114000); coastal area of Gulf of Enisey near Dixon Town, 73.482°N, 80.575°, dolerite ridge of western extremity of Byrranga Mts, rockfield with rocky tundra on a lower part of a slope, 07.VII.2017, *Fedosov 17-2-19-5* (MW0111743); vicinity of Dikson settlement, Medusa Bay, 73.334°N, 80.589°E, 26.07.2019, *Fedosov & D.E. Koltysheva* (MW9114026). ***Laptev Sea***: Preobrazheniya Island, ~74°39’N, 112°58’E, 24.VIII.1878, *F.R. Kiellman* (LE). **Republic of Sakha/Yakutia**: ***New Siberian Islands***: Bolshoi Lyakhovsky Island, sea terrace, ~73°26’N, 142°01’E, 10.VII.1956, *V.D. Aleksandrova* (LE); Kotel’nyy Island, Temp Bay, ~75°49’N, 137°35’E, 25.VIII.1947, *B.N. Gorodkov* (LE); Stolbovoi Island, 74°13’36.6"N, 135°27’39.8"E, 55 a.s.l., herb-dwarf shrub-moss tundra, 4.VIII.2019, *Czernyadjeva 20-19* (LE); [***Bulun District***]: vicinity Tiksi Settlement, ~71°35’N, 129°00’E, moss tundra, 1.IX.1955*, I.D. Kildyushevsky 59/2* (LE); ***Allaikhovsky district***: Chokurdakh village, Mount Punga, moss-herb-*Dryas* tundra, 8.VIII.1978, *V.I. Perfiljeva 16* (LE). **Chukotksky Autonomous Area**: ***Wrangel Island***: Somnitelnaya River, stream, 70°59’02.28"N, 179°91’47"W, 28.VII.2020, *R.P. Obabko* (LE); Mamontovaya River, willow-herb-moss community, 71°08’N, 179°42’W, 25.VII.1985, *O.M. Afonina* (LE); Neozhidannaya River, herb-sedge-moss community, 70°54’N, 178°50’E, 12.VII.1985, *A.I. Pulyaev* (LE). ***Chukotka***: Chukotka Plateau, Palyavaam River, dwarf shrub-sedge-moss tundra, ~68°45’N, 173°49’E, 20.VIII.1989, *S.S. Kholod* (LE B-0039721); Cape Dezhnev, 66°04’45"N, 169°39’07"W, 2.IX.1910, *A.N. Gudzenko* (LE); Erguveem River, dwarf shrub-herb tundra, 65°55’N, 175°50’W, 3.VIII.1970, *O.M. Afonina* (LE); Bay of Lawrentiya, Cape Krause, rock outcsops, 65°50’N, 171°00’W, 29.VIII.1975, *O.M. Afonina* (LE); Lake Ioni, dwarf shrub-moss tundra, ~65°53’N, 173°44’W, 21.VII.1969, *B.A. Yurtsev* (LE); Kuvet River, ~68°07’N, 170°00’E, 28.VII.1966, *Maksimenko* (LE); Chukchi Sea, Gerald Island, 71°23’N, 175°40’W, 1977, *M. Vaskovskii* (LE); vicinity of Tanyurer settlment, dwarf shrub-*Equesetum*-moss tundra, 64°50’N, 174°30’E, 7.VII.1979, *O.M. Afonina* (LE); Anadyr River basin, Ushkany mountains, sedge-moss tundra, 65°28’N, 178°50’E, 11.VIII.1978, *O.M. Afonina* (LE); Anadyr River basin, Baran’e Lake, dwarf shrub-sedge-moss tundra, 66°54’N, 175°15’E, 20.VII.1980, *O.M. Afonina* (LE); Chegitun River, horsetail-sedge-low bush-moss tundra, 66°30’N, 171°05’E, 8.VIII.1991, *O.M. Afonina* (LE); hot springs on Gilmimliveem River, hummocky spotty tundra, 65°48’N, 173°15’E, 1.VIII.1977, *O.M. Afonina* (LE).

Tortella spitzbergensis. Werner *et al.* (2014) listed several specimens of this species from Russia, but only one of them from the Arctic (Chukotka, Anadyr River basin) was proved with molecular data. We also found *T. spitzbergensis* in collections from Novaya Zemlya, northern Taimyr (Byrranga Mts and vicinity of Dickson Settlement) and in many localities in Chukotka.

Selected specimens examined: **Arkhangelsk Province:** ***Novaya Zemlya Archipelago***, South Island, north-west coast, Pankova Zemlya Peninsula, ~53°14’N, 73°06’E, 26.VIII.1947, *A.I. Zubkov* (LE B-0040279). **Krasnoyarsk Territory, Taimyrsky Dolgano-Nenetsky District:** ***Dikson Area***, Meduza Bay, 73.357°N, 80.535°E, rockfield, 25.VII.2019, *Fedosov & D.E. Koltysheva 275* (MHA9120705); same place, 73.334°N, 90.589°E, spotty tundra, 26.VII.2019, *Fedosov & D.E. Koltysheva* (MHA9120677); same place, 73.543°N, 80.658°E, N-faced rocky slope, 7.VIII.2019, *Fedosov & D.E. Koltysheva* (MHA9120657); ***Byrranga Mts***: Bikada River, *Dryas*-sedge-moss tundra, 19.VIII.1978, *M.V. Sokolova* (MW9068445); North -Eastern Taimyr, 75°15’N, 112°30’E, near Pronchczsceva Lake, submontane zone and spurs of Byrranga Range, karst complex, *Salix*-forb-moss tundra, 18.VII.1992, *E.B Pospelova* (MW9068452); Syrutaturku Lake, 73°35’N, 97°30’E, nival slope of morain hill, VIII.1994 *E.B Pospelova* (MW9068450); Byrranga Range, right bank of Bolsjaya Bootankaga River, forb-sedge spotty tundra, 8.VII.1991, *V.B. Kuvaev* 1752 (MW9068454); Ledyanaya Bay, 74.5114°N, 99.7114°E, Primetny Creek, limestone cliff, 31.VII.2004, *Fedosov Tr5* (MW9068459); same place, 74.5018°N, 99.7202°E, euthrophic scree with *Cassiope*, on turf, 31.VII.2004, *Fedosov Tr6* (MW9068461). **Chukotksky Autonomous Area**: basin of Anadyr River, Malaya Vesnovannaya River, willow-*Sphagnum* tundra, 65°20’N, 174°26’E, 14.VIII.1980, *O.M. Afonina* (LE); Anadyrsky district, upper Tanyurer River, dwarf shrub-moss tundra, 66°39’N, 176°40’E, 7.VII.1979, *O.M. Afonina* (LE); southwestern coast of Chukotka Peninsula, Provideniya district, Penkigney Bay, *Dryas*-moss tundra, 64°51’02"N, 172°49’53"W, 14.VII.2021, *O.M. Afonina* (LE B-0025502); southwestern coast of Chukotka Peninsula, vicinity of Lake Acchen, *Dryas*-herb tundra, 64°49’N, 174°55’W, 6.VII.1970, *O.M. Afonina* (LE); vicinity of Nunligran settlment, *Dryas*-herb-moss tundra, 64°49’N, 175°20’W, 6.VII.1970, *O.M. Afonina* (LE); Bay of Lawrentiya, vicinity of Lawrentiya settlment, dwarf shrub-sedge-moss tundra, 65°35’N, 171°00’W, 9.VIII.1969, *O.M. Afonina* (LE); Bay of Lawrentiya, Cape Krause, *Dryas*-willow-moss tundra, 65°50’N, 171°00’W, 19.VII.1971, *B.A. Yurtsev* (LE); vicinity of Yanrakynnot settlment, willow-sedge-moss tundra, 64°53’N, 172°30’W, 23.VII.1976, *O.M. Afonina* (LE); Arakamchechen Island, dwarf shrub-lichen tundra, 64°50’N, 172°25’W,

13.VIII.1976, *O.M. Afonina* (LE); Lake Ioni, River Ioniveem, sedge-cotton grass-moss tundra, 65°53'N, 173°44'W, 26.VII.1977, *O.M. Afonina* (LE).

Tortella cuspidatissima. Werner *et al*. (2014) studied collections of *Tortella* from Chukotka, but they did not list any specimens of *T. cuspidatissima* from this area. We found in Kamchatka and Wrangel Island several specimens that fit well this species in combination of morphological characters (stems with small central strand, costa smooth on ventral surface, juxtacostal basal cells reaching into the limb at the same height as submarginal basal cells); so we report this species for Chukotka in addition to its single known locality in Kumakhsur, lower course of Lena River provided by Köckinger & Hedenäs (2023). Three specimens of *T. cuspidatissima* from Chukotka were included into our molecular study; its results are discussed below.

Specimens examined: **Chukotksky Autonomous Area**: ***Wrangel Island***: Neizvestnaya River, *Dryas*-sedge-moss tundra, 71°13'N, 179°19'W, 15.VIII.1987, *N.A. Sekretareva* (LE); upper course of Krasnyy Flag River, *Dryas*-moss polygonal tundra, ~71°10'N, 179°04'W, 20.VIII.1938, *B.N. Gorodkov* (LE). ***Chukotka***: Pekulney Ridge, upper reaches of Buchja River, dwarf shrub-sedge tundra, 65°57'N, 174°37'E, 30.VII.1977, *A.A. Korobkov* (LE); Anadyr River basin, Ushkany mountains, willow-herb-moss tundra, 65°28'N, 178°50'E, 9.VIII.1978, *O.M. Afonina* (LE); Bay of Crest, Egvekinot settlement, in stream, 64°49'N, 175°20'W, 25.VI.1969, *O.M. Afonina* (LE); vicinity of Lake Acchen, rubbly tundra, 64°49'N, 174°55'W, 3.VIII.1970, *O.M. Afonina* (LE); Lake Pekulneyskoye, Kakanaut Bay, moss community, 62°43'N, 176°58'E, 5.VIII.1984, *O.M. Afonina* (LE); Pekulnei ridge, South Pekulneveem River, herb-moss tundra, 65°15'N, 174°31'E, 6.VIII.1979, *O.M. Afonina* (LE); vicinity of Yanrakynnot settlment, spotty tundra, 64°53'N, 172°30'W, 19.VII.1976, *O.M. Afonina* (LE); Bay of Lawrentiya, vicinity of Lawrentiya settlment, sedge-grass-moss tundra, 65°35'N, 171°00'W, 3.VIII.1969, *O.M. Afonina* (LE); Bay of Lawrentiya, Cape Krause, willow-moss tundra, 65°50'N, 171°00'W, 1.VIII.1973, *T. Belova* (LE); southwestern coast of Chukotka Peninsula, vicinity of Nunligran settlment, lake shore, 64°49'N, 175°20'W, 2.VII.1970, *O.M. Afonina* (LE); Bay of Lawrentiya, Benneta Island, hill trail, 65°45'N, 171°20'W, 21.VIII.1969, *O.M. Afonina* (LE); Arakamchechen Island, willow-herb tundra, 64°50'N, 172°25'W, 13.VIII.1976, *O.M. Afonina* (LE); Lake Ioni, River Ioniveem, dwarf shrub-moss tundra, 65°53'N, 173°44'W, 30.VI.1977, *O.M. Afonina* (LE); Chegitun River, *Dryas* tundra, 66°30'N, 171°05'W, 6.VIII.1991, *O.M. Afonina* (LE); Provideniya Bay, moss community, 64°21'N, 172°36'W, 23.VIII.2001, *O.M. Afonina P-1* (LE). [**Yakutia:**], in valle flum. Lena, Kumachsur, 70° 30′ lat. Bor. Ad rivulum in monte calcaria, 31 July 1898, *H. Nilsson-Ehle* (LE, isotype of *Tortella arctica*).

Tortella tortuosa. This species was listed almost in all regions of the Russian Arctic by Afonina & Czernyadjeva (1995). However, we confirm the presence of this species only in Polar Urals and Chukotka. It is apparently absent on the islands of Arctic Ocean; all specimens from northern Taimyr stored under this name were reidentified, mainly as *T. splendida*, as well as specimens from northern Yakutia (the latter should be also checked in SASY).

Selected specimens examined: **Yamalo-Nenets Autonomous District**: Polar Ural, middle reaches of the Sob River, railway station Sob, rocks, in a crevice between stones, ~66°50'N, 65°31'E, 8.VII.1988, *Czernyadjeva* (LE); foothills of Polar Ural, Junto Lake, herb meadow community, ~67°40'N, 68°00'E, 2.VIII.1993, *Czernyadjeva 17* (LE). **Chukotksky Autonomous Area**: Bay of Lawrentia, Krauze Cape, *Dryas-Rhododendron*-moss-lichen tundra, 31.VII.1973, *T. Belova* (LE); Nunligran Settlement outscirts, rocky slope of a hill, on fine soil, 1.VII.1970, *O.M. Afonina* (LE); basin of Velikaya River, middle course of Tamvatvaam River, moss community in stream bed on rocky slope, 23.VIII.1983, *O.M. Afonina* (LE); Provideniya District, Senyavin Straight, Penkigney Bay, Neskonon Mt., 64°51'48"N, 172°8'46"W, 160 m a.s.l., rocky stream bed, willow-sedgw-grass-moss community, *O.M. Afonina* 2321 (LE B-0038634); same district, National Park "Beringia", NW shore of Penkigney Bay near Pestsovaya River mouth, sedge-forb-*Dryas*-lichen community, 13.VIII.1978, *A.E. Katenin* (LE B-0045838); Arakamchechen Island, nival forb-horsetail-moss tundra, 13.VIII.1976, *O.M. Afonina* (LE); same place, steep rocky slope, *Dryas*-lichen community, 13.VIII.1976, *O.M. Afonina* (LE).

Tortella fleischeri (E.Bauer) J.J.Amann. Several specimens from Nenetz Autonomous District stored in LE as *T. tortuosa* attracted our attention due to the combination of leaves with abrupt, V- or U-shaped border between smooth basal cells and papillose limb cells, undulate leaf laminae, and costa smooth throughout on ventral surface. The latter character did not agree with circumscription of *T. tortuosa*, but the whole character combination fitted well *Tortella fleischeri*. In addition, in some stems central strand was observed, which also disagreed with *T. tortuosa* but fitted *T. fleischeri*. Three specimens were selected for molecular study, and their placement in *T. fleischeri* was confirmed (see below). Few specimens from Novaya Zemlya and one from Yunto Lake in Yamal were also referred to this species. Thus, *T. fleischeri* is newly recorded for the Russian Arctic (European part and Arctic West Siberia) and for the whole Russia.

Specimens examined: **Nenetz Autonomous District**: western part of ***Yugorsky Peninsula***, Sirtyayakha River, 60.847°N, 69.387°E, sedge-*Dryas* tubdra on rubble-clayish soil, 13.VIII.2008, *I.A. Lavrinenko* (LE B-0045841); ***Vaigach Island***: middle course of Sprudzhe River, 69°50'N, 59°36'E, association Carici-Dryadetum on plateau, 31.VIII.2004, *O.V. Lavrinenko* (LE); Lyamchin Bay, 69°51'00"N, 59°35'22.4"E, top of rubbly ridge, *Dryas* tundra, 9.VIII.2003, *O. Lavrinenko* (LE B-0045842); ***Dolgiy Island***: lake in the centre of island, 69°17'14"N, 58°58'30"E, Ass. Carici-Dryadetum with *Flavocetraria nivalis* on rubble-clayish soil, 23.VII.2004, *O. Lavrinenko* (LE B-0045840); Barentz Sea, ***Bolshoy Tsinkovyj Island***, 69°51'23.6"N, 59°25'00.7"E, rocky slope, 26.VIII.2020, *S.V. Sidorenko & Czernyadjeva 29-20* (LE B-0040281). **Arkhangelsk Province, Novaya Zemlya**: ***South Island***: Tschernaja Guba, near Krasino, west-facing slopes of small ridges, rubbly tundra, 4.VIII.1935, *L.I. Savicz* (LE B-0040283); NW shore, Pan'kova Zemlya peninsula, 9.IX.1947, *A.I. Zubkov* (LE B-0040284); same place, 3.IX.1947, *A.I. Zubkov* (LE B-0040285). **Yamalo-Nenetz Autonomous District**: foothills of

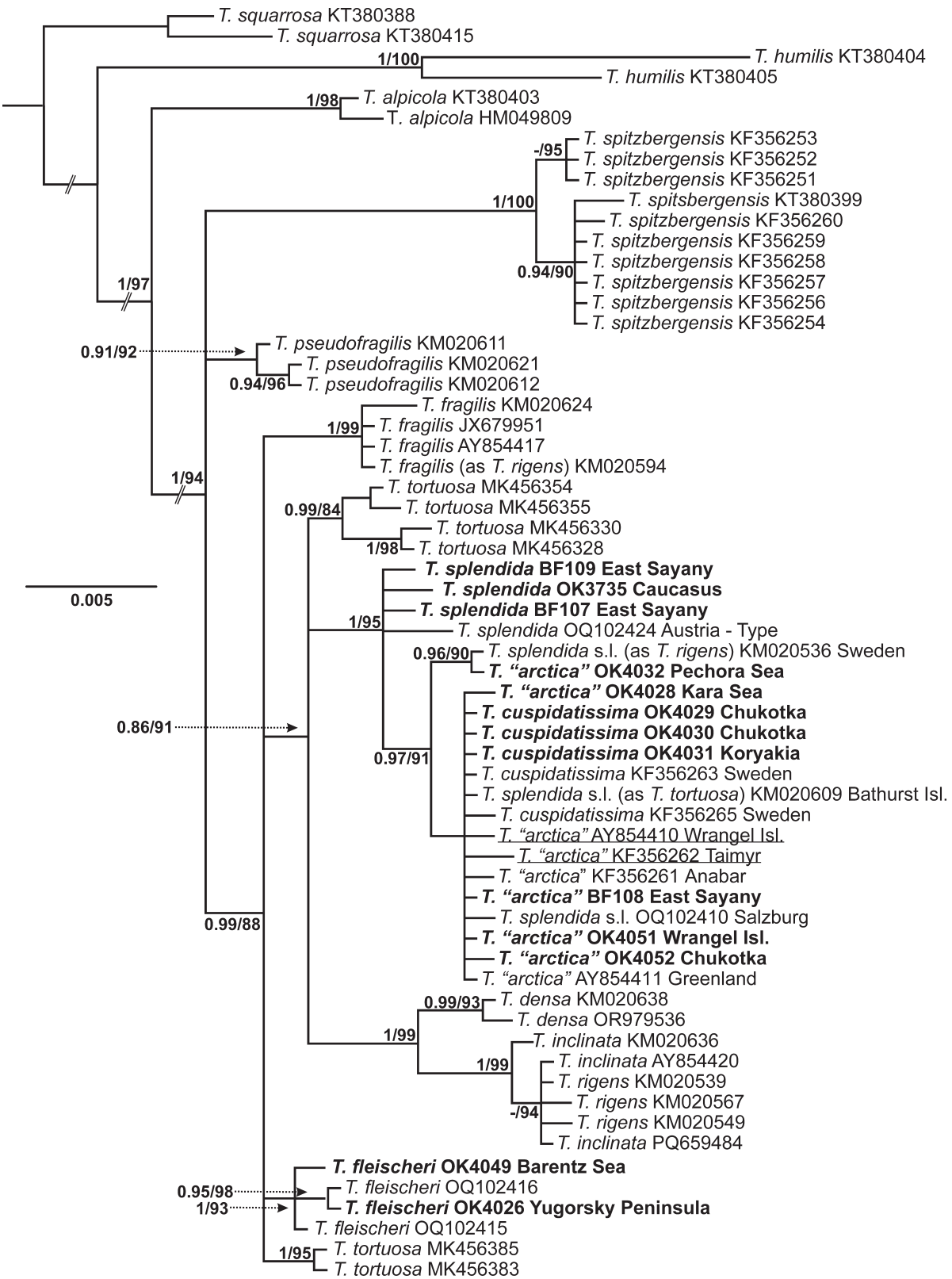

Fig. 1. Bayesian phylogenetic tree showing affinities of selected specimens of *Tortella* (newly studied specimens are boldfaced) inferred from the nr ITS sequences. Bayesian posterior probabilities (>0.7) inferred from the dataset with indels coded using simple indel coding approach and Bootstrap values (>70) obtained from 1000 pseudoreplicates of ultrafast bootstrapping as implemented in iQ-tree are shown above the branches.

Polar Ural, Junto Lake, in crevices on rock, ~67°40'N, 68°00'E, 10.VIII.1993, *Czernyadjeva 58* (LE).

Tortella densa (Lorentz & Molendo) Crundw. & Nyholm. This record is based on specimen previously reported as *T. inclinata* (Hedw. f.) Limpr. (Abramova & Stepanova, 1986). *Tortella densa* was only recently reported from Russia: Anabar Plateau (Fedosov & Ignatova, 2009) and Yakutia (Kuznetsova *et al*., 2023). Its presense in the Russian Arctic was also expected, considering a remark by Eckel (2007) who confirmed presence of *T. densa* but not of *T. inclinata* in North American Arctic.

Specimen examined: **Yakutia**, Nizhnekolymsky District, Petushki Settlement, right bank of Kolyma River, on bare soil, 69°00'N , 161°33'E, 28.VII.1984, *N.A. Stepanova* (LE).

Molecular phylogenetic study

The tree inferred from the nuclear ITS region (Fig. 1) shows reasonable resolution and support both for the clade corresponding to the particular species and the backbone topology. The ingroup represents tritomy of the (1) maximally supported *T. spitzbergensis* clade with several specimens from Russian Arctic and Subarctic studied by Werner *et al*. (2014), (2) not supported *T. pseudofragilis* (Thér.) Köckinger & Hedenäs clade and (3) weakly supported *T. tortuosa* s.l. & *T. fragilis*, *T. inclinata*/*T. rigens* Alberts. and *T. densa* clade. Within the latter four clades are found in polytomy; they correspond to (1) *T. fragilis* (PP=1, BS=99) composed of four GenBank accessions, (2) *T. fleischeri* (PP=1, BS=93), where two newly studied specimens from Russian Arctic were confirmed to belong to, (3) *T. tortuosa* p.p. (PP=1, BS=95) with two GenBank accessions, and (4) not supported clade where remaining accessions landed. Within the latter, three clades correspond to (1) remaining four Genbank accessions of *T. tortuosa* (PP=0.99, BS=84), (2) *T. densa, T. inclinata* & *T. rigens* (PP=1, BS=99), (3) *T. arctica, T. cuspidatissima* & *T. splendida* (PP=1, BS=95). Topology within the latter clade is of the particular interest, since it touches delimitation among the three species. Within it, four accessions of "*T. splendida* s.str." from the Alps, the Caucasus and the East Sayany Mountains form a grade sister to the not supported clade (PP=0.97, BS=91) which captures the remaining accessions of this species and those referred to *T. cuspidatissima* and *T. arctica*. Within the latter one, most specimens were found in not supported and not resolved polytomy, which includes all Arctic accessions of the three species, two specimens of *T. cuspidatissima* from Sweden and two specimens from mountains southwards, Austrian Alps and East Sayany. Among the latter two we could check only that from East Sayany morphologically and found it identical to the Arctic specimens, kept so far under the name *T. arctica* due to possessing combination of unistratose guide cells and limb cells weakly delimited from basal leaf cells.

DISCUSSION

The present molecular phylogenetic study was aimed mainly on confirming species identity of some problematic specimens collected in the Russian Arctic. Our dataset did not include any new samples of *T. spitzbergensis*, since its presence in Chukotka was already confirmed by Werner *et al*. (2014) and because its identification did not possess any problems. We also failed to find fresh specimens of *T. tortuosa* from the Russian Arctic suitable for DNA extracting, so its presence in Chukotka and Polar Urals is confirmed solely by morphological study. Three samples of *T. cuspidatissima* from Chukotka and Koryakia were included into the molecular dataset; however, only nrITS1-2 sequencs were obtained for them, whereas were failed to amplify DNA for sequencing chloroplast markers. Thus, their identity was only partially confirmed by molecular barcoding: in ITS this species is identical to *T. splendida*, while the analysis of chloroplast markers, according to Werner *et al*. (2014), resolves it within *T. spitzbergensis*. Here we also rely on morphological characters of plants from Chukotka, *i.e*., combination of small stem central strand; leaves with only slightly widened bases and long acumina, not twisted when dry; costa totally smooth on ventral surface; basal laminal cells gradually transiting into papillose limb cells, not extending higher along leaf margins or near costa.

At the same time, presence of *T. fleischeri* in the Arctic was not expected, and the specimens from Nenetzky Autonomous district were referred to this species because they were resolved together with two its GenBank accessions. Their morphological characters (presence of stem central strand, smooth ventral surface of costa, and sharp, V- or U-shaped transition between basal and limb cells) agree with their placement based on molecular data.

In this study, we did not specially address the problem of delimitation between arctic and non-arctic specimens of *T. splendida*. These two groups of specimens possess some differences, first of all in a number of guide cell layers in transverse secion of costa: according to Köckinger & Hedenäs (2023), alpine plants often have two layers of guide cells, at least near leaf base, while in the arctic plants guide cells are usually 1-layered, only rarely with one additional cell of the second layer (our observations). Also arctic plants usually have thicker cell walls at leaf bases, more gradually transiting into papillose limb cells than in alpine plants (as illustrated by Köckinger & Hedenäs, 2023, and based on our observation of specimens from the Caucasus). However, our molecular phylogenetic data do not confirm sharp differentiation of arctic specimens from those from southern montane regions. In the Bayesian tree obtained from our dataset, all specimens of *T. splendida* are resolved in a moderately supported (1/95) clade. It includes basal grade formed by four specimens of alpine *T. splendida* (its type from Austria, our specimen from the Caucasus, and two specimens from East Sayan Mts); they possess two layer of guide cells and thin-walled basal laminal cells. With-

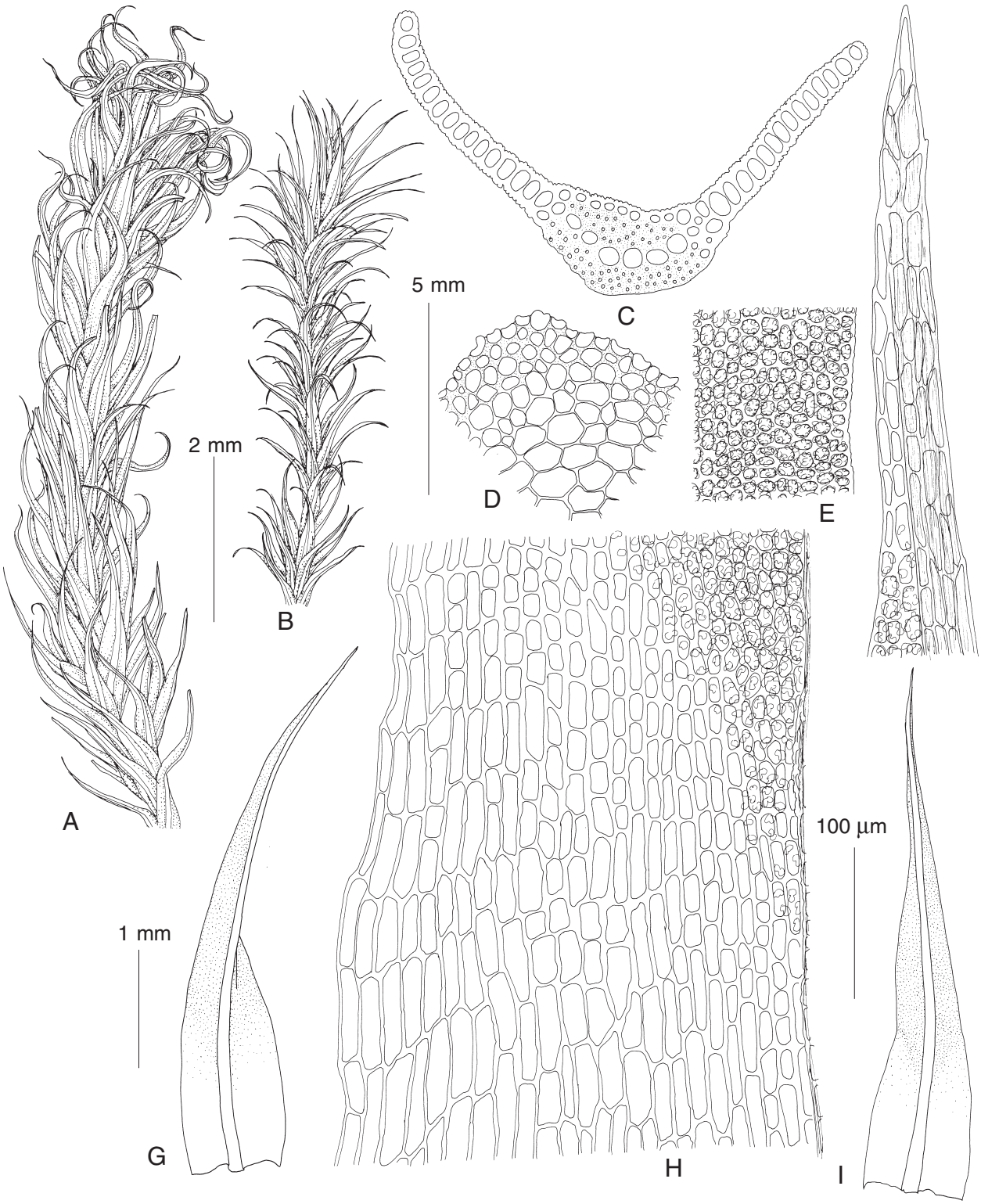

Fig. 2. *Tortella splendida* (from: Russia, Taimyr, Syrutaturku Lake, 08.1994 *Pospelova,* MW9068453). A: habit, dry; B: habit, wet; C: leaf transverse section; D: stem transverse section; E: mid-leaf cells; F: upper leaf cells; G, L: leaves; H: cells at transition zone from sheath to limb. Scale bars: 5 mm for B; 2 mm for A; 1 mm for G, I; 100 µm for C–F, H.

in this grade, a weakly supported (0.97/91) clade is nested; it contains 9 specimens from Arctic regions marked as "*T. arctica*" along with 3 specimens of *T. cuspidatissima* from Chukotka and Koryakia, one specimen from East Sayan Mts also named "*T. arctica*" due to 1-layered guide cells, and two specimens named as *T. splendida* s.l. (from Austria and Sweden). Such topology does not suggest clear delimitation between arctic and alpine plants. We could not check if specimens from Austria and Sweden also have one layer of guide cells in costa;

however, two specimens from the Tunkinskie Goltsy Range occurring nearly in the same place were resolved in different clades: first of them, with 2-layerd guide cells, appeared in the grade corresponding to "*T. splendida* s. str."; the second one, with 1-layered guide cells, got into the clade corresponding to *"T. arctica" + T. cuspidatissima*. This fact argues that the number of guide cell layers is an important character; however, in other respects morphological differentiation between arctic and alpine plants is vague. Therefore, at the moment we prefer considering *T. splendida* in a broad sense, pending an option of taxonomic consideration of *T. arctica* auct. for the special study with broader sampling.

TAXONOMY

Here we provide the descriptions, illustrations and comments on distinctive characters for *T. splendida, T. spitzbergensis, T. cuspidatissima,* and *T. fleischeri*; for *T. tortuosa* see, e.g., Köckinger & Hedenäs (2023) or Ignatov & Ignatova (2003). Key to identification also includes *T. fragilis*, *T. alpicola* and *T. densa*. Regarding two latter species, we prefer to bring an attention to them because *T. inclinata* was already recorded from the Russian Arctic, but, considering a remark by Eckel (2007) who confirmed presence of *T. densa* but not of *T. inclinata* in North American Arctic, we suppose that situation may be the same in Russia. *Tortella densa* was recently found in Taimyr (Anabar Plateau), Sette-Daban Mt. Range in Yakutia and in the Caucasus, Dagestan. It usually grows in treeless habitats: steppe communities, heaths, rocky mountain tundra, on screes, mainly on calcareous substrates.

Tortella splendida Köckinger & Hedenäs, Lindbergia 2023(e24903): 20, 8G–J, 11. 2023. Fig. 2, 6B, G.

Plants medium-sized to large, on loose or dense cushions, light green, yellowish-green or rusty-brownish. *Stems* to 6 cm long, irregularly branched, densely foliose, weakly tomentose, round in transverse section, without central strand. *Leaves* 3.0–4.5(–7).0×0.6–1.2 mm, lanceolate or linear-lanceolate, with length:width ratio 5–7:1, lower leaves erect-spreading when dry, upper leaves incurved and slightly twisted; erect-spreading to widely spreading when wet, straight from above view, limbs gradually narrowed upwards, narrowly acuminate at apex, not cucullate, canaliculate distally; leaf bases short or elongate-rectangular, not or slightly widened, without distinct shoulders; leaf margins plane or widely incurved distally, entire, not undulate; *costa* strong, (75–) 100–150(–200) μm wide at leaf base, gradually tapering distally, excurrent into short, weakly denticulate mucro, with quadrate, papillose cells on ventral surface from above base, with elongate, smooth cells on dorsal surface or with few spinulae, in transverse section with 1(2) layers of guide cells, 2 stereid bands, differentiated ventral epidermis and weakly differentiated dorsal epidermis; lamina unistratose, rarely with few bistratose spots; *upper and median laminal cells* rounded-quadrate, 7–11 (–13) μm wide, thick-walled, densely papillose, papillae low, obscuring cell walls; *basal laminal cells* oblong-rectangular, thick- or moderately thin-walled, smooth, yellowish, basal marginal cells often narrower than central and juxtacostal cells; boundary between basal and limb cells usually gradual, U-shaped, rarer abrupt, V-shaped. *Dioicous*, sporophytes unknown.

Distribution and ecology. *Tortella splendida* is an arcto-alpine species, occuring in Asian and North American Arctic regions, in the mountains of Central Europe (Köckinger & Hedenäs, 2023), Caucasus (Kuznetsova *et al*., 2023), southern Siberia, Russian Far East (our data), China (Eckel, 2007), and in North America in Colorado and Maine (Eckel, 2007). It is common in northern Taimyr and Chukotka, especially on Vrangel Island. It grows on gravelly soil, in niches between rocks of rockfields, rock crevices, on rocks outcrops, especially in areas with calcareous bedrocks; it also occurs along brooks and in polygonal and spotty tundra, where it forms large pure fufts or grows among other mosses.

Differentiation. *Tortella splendida* is similar to *T. tortuosa* in having leaves with costa papillose on ventral surface and stems lacking central strand. However, its leaves are straight when wet (usually sigmoid and often secund in *T. tortuosa*); their limbs are gradually narrowing from above base (limbs have parallel margins for a long distance in *T. tortuosa*); leaf margins are not wavy (usually strongly wavy in *T. tortuosa*); transition between basal and limb cells is gradual (mostly abrupt, V-shaped in *T. tortuosa*), elongate basal cells do not extending high along leaf margins (reach far up in *T. tortuosa*); it also has less tomentose stems (often densely tomentose in *T. tortuosa*). Basal cells are usually yellowish in arctic plants of *T. splendida*, contrary to white basal cells of *T. tortuosa*. Unlike *T. splendida*, *T. tortuosa* never possess two layers of guide cells in costa. There is some similarity in leaf shape between *T. splendida* and *T. cuspidatissima*, but the latter species can be readily separated by having leaf costae smooth ventrally and stems with weak central strand. Also in *T. splendida* on average cells in the upper part of the leaf are smaller (7–11 μm vs 11–16 μm in *T. cuspidatissima*) and costa is wider (100–150(–200) μm vs 50–100 (120) μm in *T. cuspidatissima*).

Tortella spitsbergensis (Bizot & Thér.) O. Werner, Köckinger & Ros, Nova Hedwigia 98(3–4): 287. 2014. — *Grimmia spitsbergensis* Bizot & Thér., Bull. Sci. Bourgogne 5: 70. 71. 1935. Fig. 3, 6D, I.

Plants medium-sized to large, in dense tufts, yellowish-green or brownish, dull. *Stems* to 6 cm long, irregularly branched, densely or sparsely foliate, more or less tomentose, triangular or round in transverse section, with large, sharply delimited central strand, consisting of small, thinner-walled cells. *Leaves* (2.0–)2.5–3.5(–4.0) ×0.4–0.7 mm, with ovate bases and lanceolate limbs, contorted and twisted when dry, erect-spreading, often with recurved acumina when wet, sigmoid, gradually tapered

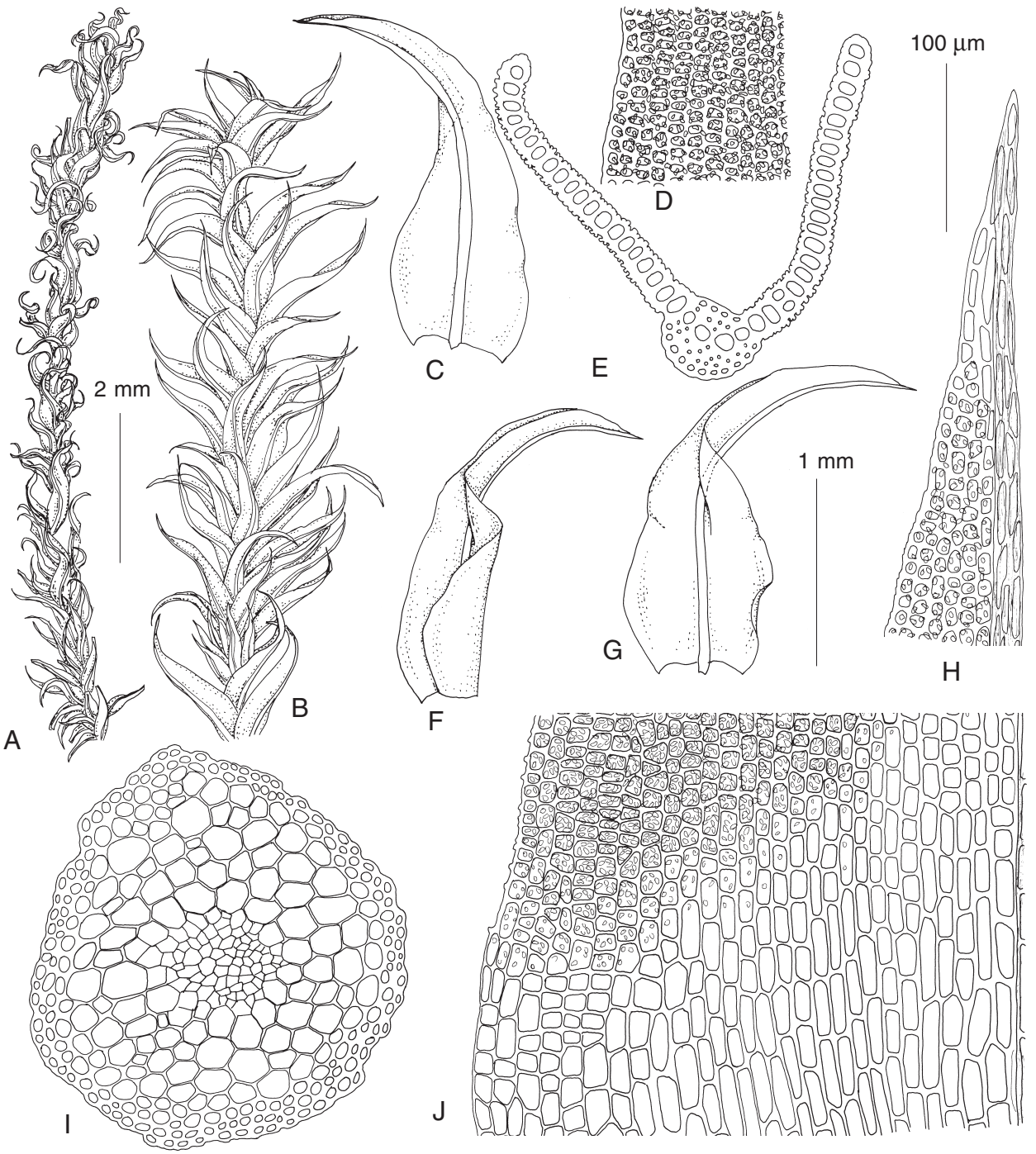

Fig. 3. *Tortella spitsbergensis* (from: Russia, Taimyr, near Pronchczsceva Lake, 18.07.1992 *Pospelova,* MW9068452). A: habit, dry; B: habit, wet; C, F, G: leaves; D: mid-leaf cells; E: leaf transverse section; H: upper leaf cells; I: stem transverse section; J: cells at transition zone from sheath to limb. Scale bars: 2 mm for A–B; 2 mm for A; 1 mm for C, F, H; 100 µm for D–E, G, I–J.

distally, narrowly acuminate, not cucullate at apex; widely keeled in midleaf; leaf bases wide-elliptic, well differentiated, wider than limb, with or without distinct shoulders; margins plane in mid-leaf and widely incurved above, entire, slightly wavy; *costa* strong, 50–75(–110) µm wide at leaf base, gradually tapering upwards, on ventral and dorsal surfaces with elongate, smooth cells, excurrent into long, smooth mucro, in transverse section with 1 layer of guide cells, two stereid bands, ventral epidermis not or weakly differentiated, dorsal epidermis differentiated; lamina unistratose; *upper and median laminal cells* rounded-quadrate and transverse elliptical, 8–11(–13) µm wide, thick-walled, densely papillose, papillae low, not obscuring cells walls; laminal cells in central and juxtacostal part of leaf base elongate-rectangular, thick-walled, smooth, yellowish, basal marginal cells considerably shorter and wider in the widest part of leaf base, forming pellucid area; transition from smooth bas-

al cells and papillose limb cells gradual, border W-shaped, smooth cells reach into limb higher near costa than at leaf margins. *Dioicous*, sporophytes unknown.

Distribution and ecology. This species was described from Spitzbergen (Norway). In Russian handbooks and check-lists it was provided under the name *Trichostomum cuspidatissimum* (Savicz-Lyubitskaya & Smirnova, 1970; Ignatov *et al.*, 2006). Werner *et al*. (2014) also confirmed the presence of *Tortella spitzbergensis* Canada (Newfoundland) and in Russia (Arctic Siberia and Chukotka). In the course of our study, we found it to occur on Novaya Zemlya and being common on Northern Taimyr and Chukotka. Outside Arctic, it is known in Russia in Anabar Plateau, Yakutia, Magadan Province, Kamchatka, Khabarovsk and Zabaikalsky Territories, Buryatia and Tyva. It grows in wet arctic and mountain tundra, boggy sites, on rocky slopes, screes, wet rock outcrops, often on calcareous rocks.

Differentiation. *Tortella spitzbergensis* differs from all other species of the genus in having large, sharply delimited stem central strand; it is formed of very thin-walled, numerous small cells surrounded by firm-walled cells of central cylinder. Presence of stem central strand, costa smooth on ventral surface, leaves with wide-ovate bases and comparatively short, lanceolate acumina differentiate *T. spitzbergensis* from *T. splendida*. *Tortella cuspidatissima* possesses stem central strand, but the small one; it also has gradual transition between basal and limb cells, but its juxtacostal basal cells reach into the limb at the same height as the marginal ones; its basal marginal cells are only slightly wider than central cells, of the same width or narrower.

Tortella cuspidatissima (Cardot & Thér.) O. Werner, Köckinger & Ros, Nova Hedwigia 98(3–4): 287. 2014. — *Trichostomum cuspidatissimum* Cardot & Thér., Proc. Wash. Acad. Sci. 4: 302. 13 f. 4. 1902. Fig. 4, 6C, H.

Plants medium-sized to large, in loose or dense tufts or cushions, yellowish-green or brownish. *Stems* to 6 cm long, irregularly branching, densely foliate, weakly tomentose, round in transverse section, with weak, occasionally indistinct or, rarely, absent central strand. *Leaves* 2.5–3.5(–4.0)×0.7–0.9 mm, linear-lanceolate, with length:width ratio 4–6:1, flexuose, occasionally slightly twisted when dry, erect-spreading or patent when wet, sigmoid, limb gradually tapered, narrowly acuminate, not cucullate, keeled above; leaf bases short rectangular or ovate, slightly widened, with indistinct or distinct shoulders; margins plane in mid-leaf, widely incurved above, entire, slightly wavy; *costa* moderately strong, 50–100 (–120) μm wide at leaf base, gradually narrowing distally, on ventral and dorsal surfaces with elongate, smooth cells, excurrent into moderately long, smooth or weakly denticulate mucro, in transverse section with one layer of guide cells, two stereid bands, ventral epidermis differentiated, dorsal epidermis weakly differentiated; lamina unistratose; *upper and median laminal cells* rounded-quadrate, (7–)11–14(–16) μm wide, thick-walled, densely papillose, papillae low, obscuring cell walls; basal laminal cells elongate-rectangular, moderately thick-walled, smooth, yellowish, reaching into the limb at equal height near costa and at margins, gradually transiting into limb cells; basal marginal cells wider or narrower than central basal cells. *Dioicous*, sporophytes unknown.

Distribution and ecology. *Tortella cuspidatissima* was described from Hall Island near NW coast of North America, which remains its only known locality in this continent. Werner *et al*. (2014) considered it as a species of hybrid origin with parent species *T. arctica* (=*T. splendida*) and *T. spitzbergensis*. They also found it in Sweden. Köckinger & Hedenäs (2023) referred to *T. cuspidatissima* type specimens of *T. arctica* from the lower course of Lena River. We also found it in herbarium collections from Chukotka and Vrangel Island. It grows on soil in wet arctic tundra, on moist calcareous rocks with soil layer, along streams, and on pebbly sea shore terrace.

Differentiation. *Tortella cuspidatissima* differs from *T. tortuosa* and *T. splendida* by presence of stem central strand (though occasionally indistinct) and smooth costa on ventral surface, and from the former species also by gradual transition between basal and limb cells. Small central strand, 2–4 cells wide, differentiates *T. cuspidatissima* from *T. spitzbergensis* (in the latter species central strand is usually very conspicuous, large, 7–14 cells wide, only very rarely ±small). In *T. cuspidatissima* stems are round in transverse section, while in *T. spitzbergensis* they are triangular in outline. Basal cells reach into the limb at equal height at margins and near costa in *T. cuspidatissima*, but higher near costa in *T. spitzbergensis.* In *T. cuspidatissima* basal marginal cells are narrower or lightly wider than central cells, whereas in *T. spitzbergensis* several marginal cell rows at leaf base are distinctly wider and shorter, forming pellucid area. An additional character is the width of upper and median laminal cells: (7–)11–14(–16) μm in *T. cuspidatissima* vs. 8–11(–13) μm in *T. spitzbergensis*. *Tortella fleischeri*, with also posesses weak central strand and costae smooth ventrally, can be distinguished by abrupt transition between basal and limb cells (Fig. 6).

Tortella fleischeri (E. Bauer) J.J. Amann, Beitr. Kryptogamenfl. Schweiz 7(2): 30. 1933. – *Trichostomum fleischeri* E. Bauer, Musci Eur. Exsic. 15: no. 741. 1910. Fig. 5, 6E, J.

Plants small to medium-sized, in dense, easily separated tufts, light-green, yellowish-green or rusty-brownish. *Stems* to 6 cm long, irregularly branched, densely foliate, weakly tomentose, round or triangular in transverse section, with distinct or weak central strand. *Leaves* 2.0–5.0(–7.0)×0.5–1.0 mm, lanceolate or linear-lanceolate, with length:width ratio 4–7:1, twisted around their axis or contorted when dry, erect-spreading to recurved when wet, occasionally secund, sigmoid, limbs gradually narrowed distally, narrow acuminate at apex,

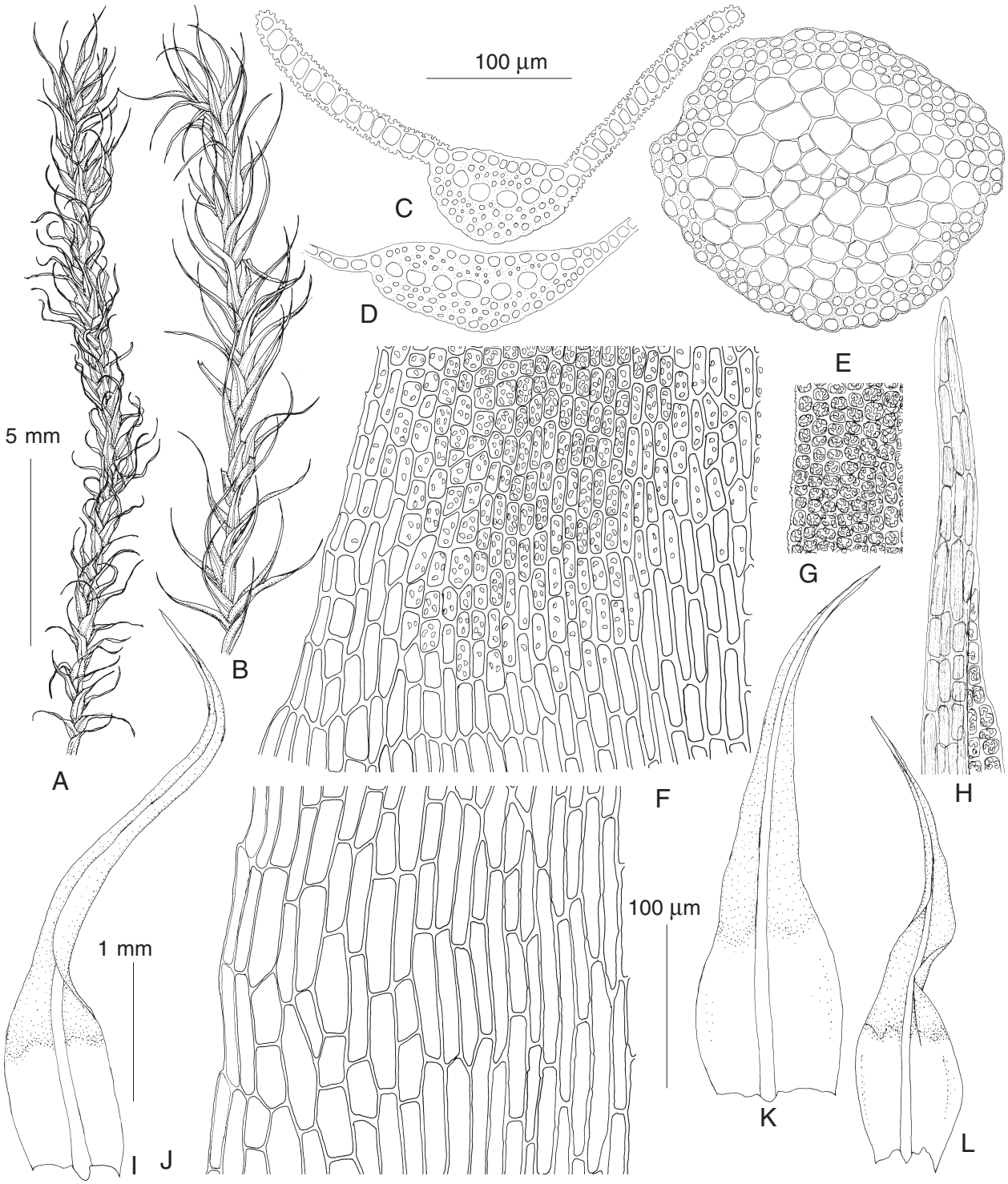

Fig. 4. *Tortella cuspidatissima* (ffrom: Russia, Chukotka, Malaya Vesnovannaya river, 15.VIII.1980, *Afonina,* LE). A: habit, dry; B: habit, wet; C–D: leaf transverse sections; E: stem transverse section; F: cells at transition zone from sheath to limb; G: mid-leaf cells; H: upper leaf cells; I, K–L: leavs; J: basal leaf cells. Scale bars: 5 mm for A–B; 1 mm for I, K–L; 150 µm for C–E; 100 µm for F–H, J.

not cucullate, keeled above; leaf bases quadrate, moderately widened; margins plane in mid-leaf, widely incurved above, entire, wavy; *costa* strong, 60–140 µm wide at base, gradually narrowing distally, with elongate, smooth cells on ventral surface at least in midleaf, on dorsal surface with elongate, not papillose cells, with few spinulae, excurrent into long, sharply dentate mucro, in transverse section in 1 layer of guide cells, 2 stereid bands, with narrow band of undifferentiated ventral epidermis in the centre, dorsal epidermis not differentiated; lamina unistratose; *upper and median laminal cells* rounded-quadrate, 8–12 µm wide, thick-walled, densely papillose,

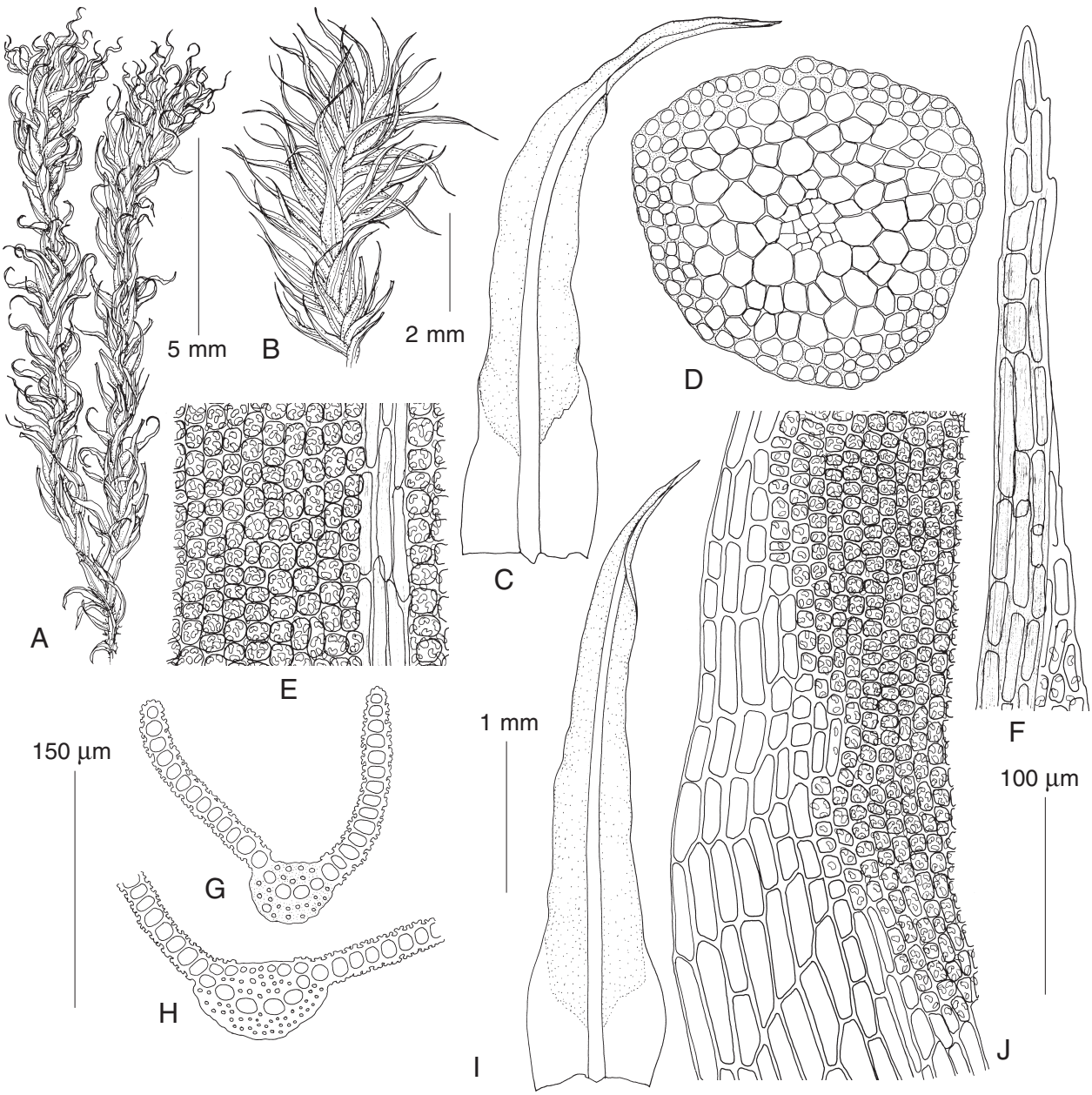

Fig. 5. *Tortella fleischeri* (from: Russia, Nenetz Autonomous District, 13.VIII.2008, *I.A. Lavrinenko*, LE B-0045841). A: habit, dry; B: habit, wet; C, I: leaves; D: stem transverse section; E: mid-leaf cells and ventral surface of costa; F: upper leaf cells; G–H: leaf transverse sections; J: cells at transition zone from sheath to limb. Scale bars: 5 mm for A–B; 1 mm for I, K–L; 150 µm for C–E; 100 µm for F–H, J.

papillae massive, not obscuring cell walls; basal laminal cells elongate-rectangular, moderately thick- or thin-walled, smooth, hyaline or yellowish; transition between basal and limb cells abrupt, V-shaped, or more or less gradual, U-shaped. *Dioicous*, sporophytes very rare, in the territory of Russia unknown.

Distribution and ecology. This species was described from Austria. Köckinger & Hedenäs (2023) characterize it as calciphilous and cryophilous species, usually growing above tree line. Outside the Alps, they report it from Slovakia, Montenegro, and Scotland, considering its presence in the latter locality as surprising, as it is usually substituted in the north of Europe by ecologically similar *T. cuspidatissima* and *T. spitzbergensis*. Nevertheless, in Russia it was discovered in the northeastern European part, where *T. cuspidatissima* was not found and *T. spitzbergensis* was recorded only on Novaya Zemlya. *Tortella fleischeri* was identified in collections from Nenetz Autonomous district, on Yugorsky Peninsula and Vaigach Island. It was also revealed in collections from Novaya Zemlya (belongs to Arkhangelsk Province) and Yamalo-Nenets Autonomous District in the north of West Siberia.

According to the label data, *Tortella fleischeri* grew on gravely substrate in different types of tundra.

Differentiation. Specimens from Russia were stored in herbaria under the names *T. tortuosa* and *T.* cf. *arcti-*

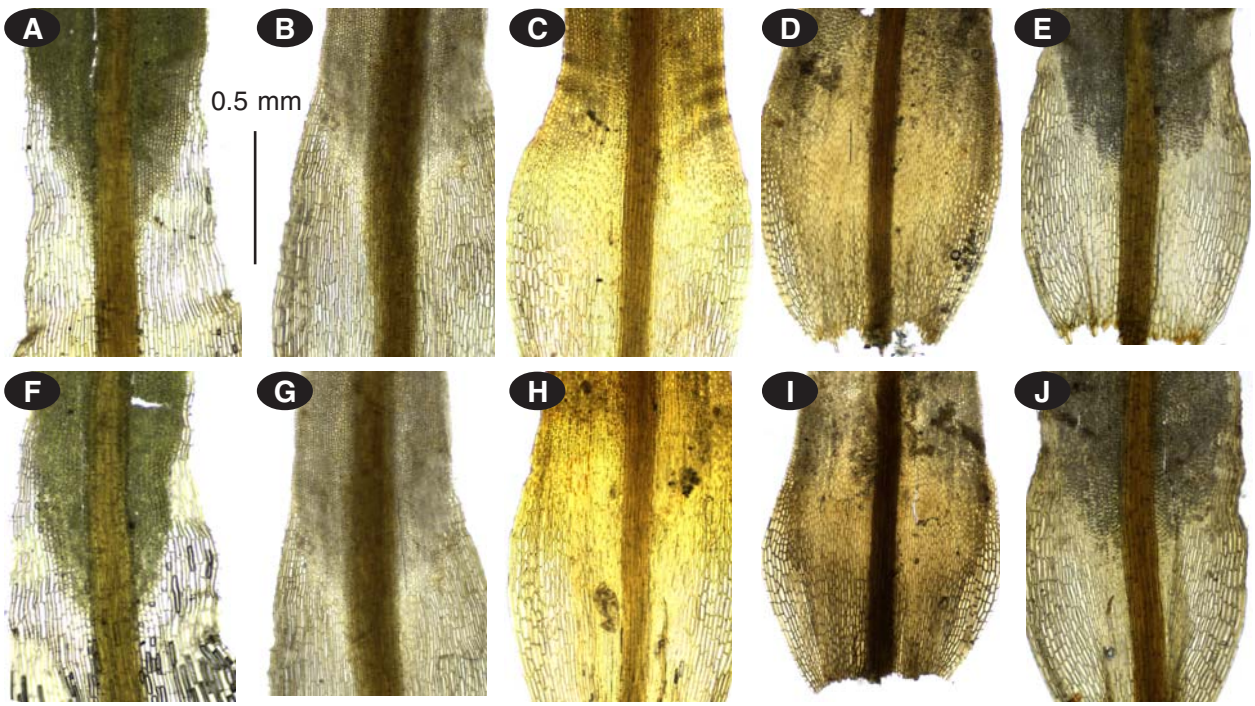

Fig. 6. Basal leaf areolation of *Tortella* species. A, F: *Tortella tortuosa* (Chukotka, 17.VII.2021 *Afonina 2321*, LE); B, G: *T. splendida* (Nordenshelda Archipelago, 6.IX.2023, *Czernyadjeva 30-23*, LE); C, H: *T. cuspidatissima* (Chukotka, 15.VIII.1980 *Afonina s.n.*, LE); D, I: *T. spitsbergensis* (Novaya Zemlya, 26.VIII.1947 *Zubkov s.n.*, rel 13, LE); E, I: *T. fleischeri* (Bolshoi Zinkovy Island, 26.VIII.2020, *Sidorenko & Czernyadjeva 29-20*, LE).

ca. From both these species *T. fleischeri* differs by presence of stem central strand (however, sometimes indistinct) and narrow strip of smooth cells along ventral surface of costa. From *T. cuspidatissima* and *T. spitzbergensis,* which also have stem central strand and costa smooth ventrally, *T. fleischeri* (at least specimens from Russian Arctic) differ in having abrupt, V- or U-shaped transition between basal and limb cells (Fig. 6).

Tortella tortuosa (Hedw.) Limpr., Laubm. Deutschl. 1: 604. 1888. — *Tortula tortuosa* Hedw., Sp. Musc. Frond. 124. 1801.

This species is widespread throughout Holarctic (it is absent only in areas without rocky substrates), as well as in Central and South America. It is common in mountain areas of Russia and found in some its lowland provinces. However, in Russian Arctic it is substituted by other species of the genus: *Tortella fleischeri* in European part and Novaya Zemlya, *T. splendida, T. cuspidatissima*, and *T. spitzbergensis* in Asian sector of the Arctic, except Chukotka, where it is not rare and may co-occur with aforementioned species. Few specimens from Polar Ural (Yamalo-Nenetz Autonomous District) also belong to *T. tortuosa*. This species is readily recognized by combination of such characters as stems lacking central strand; leaves with parallel margins at mid-leaf, contorted and crisped when dry, wavy at margins, with costa papillose on ventral surface, and usually thin-walled, hyaline basal cells, abruptly delimited from limb cells with v-shaped boundary, reaching high up along margins. Its distinctions from other species of the genus occurring in Rissian Arctic are discussed in comments to these species.

Key to identification of *Tortella* species in the Russian Arctic

1. Leaves fragile; leaf apices modified, propaguloid, regularly broken off 2
— Leaves not or irregularly fragile; leaf apices not modified 3
2. Stems with differentiated central strand; propaguloid leaf apices with several clear constrictions, divided into short barrel-shaped fragments; adaxial surface of costa formed of quadrate, papillose cells; basal laminal cells snow-white hyaline; border of smooth narrow cells at upper leaf margins absent .. .. *T. alpicola*
— Stem central strand not differentiated; propaguloid apices without or with few constrictions; adaxial surface of costa formed of elongate, smooth cells; basal laminal cells yellowish; border of 1–2 rows of smooth narrow cells at upper leaf margins often present .... *T. fragilis*
3. Costa with quadrate, papillose cells on ventral surface from above base; central strand absent 4
— Costa elongate cells on ventral surface, smooth throughout; central strand absent or present 5
4. Leaves usually not undulate when wet; transition between smooth, yellowish basal cells and papillose limb cells gradual, U-shaped ..... *T. splendida*

— Leaves undulate at margins when wet; transition between smooth, hyaline basal cells and papillose limb cells abrupt, V-shaped ..... *T. tortuosa*

5. Leaves oblong-lanceolate, acute at apex; upper and median laminal cells with high, pedunculate papillae; stem central strand absent ..... *T. densa*

— Leaves linear-lanceolate, gradually narrowed to the apex, acuminate; upper and median laminal cells with low papillae; stem central strand usually present, rarely indistinct or absent 6

6. Smooth basal laminal cell extend upwards higher along leaf margins than near the costa, forming hyaline border; transition between smooth limb cells and papillose laminal cells ±sharp, V- or U-shaped ..... *T. fleischeri*

— Smooth basal laminal cell extend upwards higher near the costa than along leaf margins or at equal height; transition between smooth limb cells and papillose laminal cells gradual 7

7. Stems with large central strand, 6–15 cells wide; smooth basal laminal cell extend upwards higher near the costa than along leaf margins; cells near margins in several rows hyaline, wider than juxtacostal cells, forming a distinct border; upper laminal cells 8–11(–13) μm wide ..... 12. *T. spitzbergensis*

— Stems with slender central strand 3–4 cells wide; smooth basal laminal cell extend upwards equally high near the costa and at leaf margins; basal marginal cells equal in width or slightly wider than juxtacostal cells, not forming a distinct border; upper laminal cells (7)11–14(16) mm wide ..... *T. cuspidatissima*

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LITERATURE CITED

[ABRAMOVA, A.L. & N.A. STEPANOVA] АБРАМОВА А.Л., Н.А. СТЕПАНОВА 1986. К флоре мхов нижнего течения р. Колымы. – [On the moss flora of the lower course of Kolyma River] *Новости систематики низших растений* [*Novosti Sistematiki Nizshikh Rastenij*] **23**: *208–214.*

AFONINA, O.M. & I.V. CZERNYADJEVA 1995. Mosses of the Russian Arctic: check-list and bibliography. – *Arctoa* **5**: *99–142.*

FEDOSOV, V.E. & E.A. IGNATOVA. 2009. On *Tortella densa* (Lorentz & Molendo) Crundwell & Nyholm (Pottiaceae, Musci) in Russia. – *Arctoa* **18**: *189–194*.

ECKEL, P.M. 2007. *Tortella*. *– In: Flora of North America Editorial Committee (eds.) Flora of North America North of Mexico Vol. 27. Oxford University Press, New York, pp. 498–511.*

GARDINER, A., M. IGNATOV, S. HUTTUNEN & A. TROITSKY. 2005. On resurrection of the families Pseudoleskeaceae Schimp. and Pylaisiaceae Schimp. (Musci, Hypnales). – *Taxon* **54**: *651–663*.

HALL, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. – Nucleic Acids Research Symposium Series **41**: *95–98.*

MÜLLER, K. 2005. SeqState. – *Applied Bioinformatics* **4**: *65–69*.

IGNATOV, M.S., O.M. AFONINA & E.A. IGNATOVA *et al.*. 2006. Checklist of mosses of East Europe and North Asia. – *Arctoa* **15**: *1–130.*

[IGNATOV, M.S. & E.A. IGNATOVA] ИГНАТОВ М.С., Е.А. ИГНАТОВА 2003. Флора мхов средней части европейской России. Т. 1. – [Moss flora of the Middle European Russia. Vol. 1] *M., KMK* [*Moscow, KMK*]: *1–608.*

KÖCKINGER, H. & L. HEDENÄS. 2023. The supposedly well-known carbonate indicator *Tortella tortuosa* (Pottiaceae, Bryophyta) split into eight species in Europe. – *Lindbergia* 2023: e24903 [1–35].

KUZNETSOVA, O.I., A.V. FEDOROVA, V.E. FEDOSOV, E.A. IGNATOVA, M.S. IGNATOV & YU.S. ISHCHENKO. 2023. Bryophyte molecular barcoding records. 9. – *Arctoa* **32**(2): *264–268*.

OTNYUKOVA, T.N., E.A. IGNATOVA, M.S. IGNATOV & V.E. FEDOSOV. 2004. New record of *Tortella alpicola* Dix. in Eurasia. – *Arctoa* **13**: *197–201*.

RAMBAUT, A., A.J. DRUMMOND, D. XIE, G. BAELE & M.A. SUCHARD. 2018. Posterior Summarization in Bayesian Phylogenetics Using Tracer 1.7. – *Systematic Biology* **67**: *901–904*.

RONQUIST, F., M. TESLENKO, P. VAN DER MARK, D.L. AYRES, A. DARLING, S. HÖHNA, B. LARGET, L. LIU, M.A. SUCHARD & J.P. HUELSENBECK. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. – *Systematic Biology* **61**: *539–542*.

[SAVICZ-LYUBITSKAYA, L.I. & Z.N. SMIRNOVA] САВИЧ-ЛЮБИЦКАЯ Л.И., З.Н. СМИРНОВА. 1970. Определитель листостебельных мхов СССР. Верхоплодные мхи. – [Handbook of mosses of the USSR. The acrocarpous mosses] *Л., Наука* [*Leningrad, Nauka*], *822 pp.*

SIMMONS, M.P. & H. OCHOTERENA. 2000. Gaps as Characters in Sequence-Based Phylogenetic Analyses. – *Systematic Biology* **49**: *369–381*.

TRIFINOPOULOS, J., L.T. NGUYEN, A. VON HAESELER & B.Q. MINH. 2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. – *Nuclear Acids Research* **44** (W1): W232-W235. doi: 10.1093/nar/gkw256

WERNER, O., H. KÖCKINGER, M. MAGDY & R. M. ROS. 2014. On the systematic position of *Tortella arctica* and *Trichostomum arcticum* (Bryophyta, Pottiaceae). – *Nova Hedwigia* **98**(3–4): *273–293*.

[YURTSEV, B. A., A. I. TOLMATSCHEV & O. V. REBRISTAYA] ЮРЦЕВ, В. А., А. И. ТОЛМАЧЕВ, О.В. РЕБРИСТАЯ. 1978. Флористическое ограничение и разделение Арктики. – [The floristic delimitation and subdivision of the Arctic] *В кн.: Арктическая флористическая область* [*In: The Arctic Floristic Region*] *Л., Наука* [*Leningrad: Nauka*], *pp. 9–104*.

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Appendix 1. Voucher data and GenBank accession numbers for newly sequenced specimens.

Species	Isolate	Locality	Specimen_voucher	ITS
Tortella densa	OK4050	Russia: Dagestan Gunib	M. Ignatov & E. Ignatova 09-252 (MW9067640)	PQ659483
Tortella inclinata	OK3740	Russia: Irkutsk Province	V. Fedosov & D. Koltysheva 18-2-42 (MW9092499)	PQ659484
Tortella fleischeri	OK4026	Russia: Nenetz Autonomous District, Yugorsky Peninsula	13 Aug 2008, I.A. Lavrinenko (LE B-0045841)	PQ659485
Species	Isolate	Locality	Specimen voucher	ITS
Tortella splendida	OK4028	Russia: Kara Sea, Bianka Island	I.V. Czernyadjeva 30-23 (LE)	PQ659486
Tortella cuspidatissima	OK4029	Russia: Chukotka	9 Aug 1978, O.M. Afonina (LE)	PQ659487
Tortella cuspidatissima	OK4030	Russia: Chukotka	15 Aug 1980, O.M. Afonina (LE)	PQ659488
Tortella cuspidatissima	OK4031	Russia: Koryakia	5 Aug 1984, Afonina (LE)	PQ659489
Tortella fleischeri	OK4049	Russia: Barentz Sea, Bolshoy Tsinkovyj Island	S.V. Sidorenko & I.V. Czernyadjeva 29-20 (LE B-0040281)	PQ659490
Tortella splendida	OK4051	Russia: Wrangel Island	25 July 2020 R.P. Obabko (LE B0024343)	PQ659491
Tortella splendida	OK4052	Russia: Chukotka	27 Aug 2001, O.M. Afonina (LE)	PQ659492
Tortella tortuosa	OK3732	Russia: Primorsky Territory	Fedosov & Pisarenko Exs. 103 (MW9110719)	PQ659493
Tortella tortuosa	OK3733	Russia: Buryatia, Tunkinski Distr.	Seregin 2007 M-1974 (MW 9067619)	PQ659494
Tortella commutata	OK3737	Russia: Ingushetia	Ignatov et al. 18-859 (MHA9026361)	PQ659495
Tortella tortuosa	OK3738	Russia: Yakutia	Ignatov & Ignatova 15-78 (MHA9110233)	PQ659496
Tortella tortuosa	OK3741	Russia: Primorsky Territory	Ignatov et al. 13-1896 (MW9067629)	PQ659497
Tortella commutata	OK3742	Russia: Yakutia, Orulgan	Ignatov 11-4141 (MHA9067625)	PQ659498
Tortella commutata	OK3736	Russia: Dagestan, Gunib	Fedosov 10-2-138 (MW9067478)	PQ659499
Tortella splendida	BF107	Russia: Buryatia, Tunkinski Distr.	Fedosov (MW9131305)	PQ659500
Tortella splendida	BF108	Russia: Buryatia, Tunkinski Distr.	Fedosov (MW9131309)	PQ659501
Tortella splendida	BF109	Russia: Buryatia, Tunkinski Distr.	Fedosov (MW9131299)	PQ659502
Tortella splendida	OK3735	Russia: Severnaya Ossetia	Korotkov 21 Aug 2004 (MW9067487)	PQ659503