BRYOPHYTES — МОХООБРАЗНЫЕ

Gyrothyraceae (Marchantiophyta) — a new family for the Russian liverwort flora

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Abstract. *Gyrothyra underwoodiana* is the only species of a peculiar monotypic family, a remarkable western North American endemic. Recent exploration has revealed *Gyrothyra* at the western end of the Commander-Aleutian Island Chain (Bering Island), and this is the first record of the taxon in Russia. The species was collected in four localities in various parts of the island and these findings formally emphasizes the West-North American connections of the flora of the Commander Islands. However, the distribution patterns of *Gyrothyra* in other Aleutians may suggest the adventive character of occurrence of the species on Bering Island. The morphological description and illustrations of *G. underwoodiana* based on specimens from Bering Island, as well as discussion on its ecology, morphology and distribution are provided.

Keywords: *Gyrothyra*, Hepaticae, Aleutians, Bering Island, Commanders, North Pacific Arc.

Gyrothyraceae (Marchantiophyta) — новое семейство для флоры печеночников России

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Резюме. *Gyrothyra underwoodiana* — единственный вид своеобразного монотипного семейства, — типичный западно-североамериканский эндем. В результате недавних исследований *Gyrothyra* был обнаружен на западной оконечности Алеутской островной дуги (остров Беринга, Командорские острова), что является первой находкой таксона в России. Вид был собран в четырех точках в разных районах острова и эти находки формально подчеркивают западно-североамериканские связи флоры Командорских островов. Тем не менее, особенности распространения *G. underwoodiana* на других Алеутских островах могут свидетельствовать об адвентивном характере распространения вида на о. Беринга. Представлены морфологическое описание и рисунки, сделанные на основе собранных материалов, а также обсуждение экологии, морфологии и особенностей распространения *Gyrothyra*.

Ключевые слова: *Gyrothyra*, Hepaticae, Алеуты, Командоры, остров Беринга, Северная Пацифика.

Gyrothyra underwoodiana M. Howe as the only species of the monotypic genus was described by M. A. Howe (1897) based on specimens from California and Washington,

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U.S.A. Later it was put into newly segregated family Gyrothyraceae (Schuster, 1951, 1970). The latter is a peculiar monotypic family genetically related to the monotypic Arnelliaceae and oligogeneric Harpanthaceae (Shaw *et al*., 2015; Forrest *et al*., 2006). This is a shining example of an endemic taxon with a "North Pacific Arc distribution" (Hong, 1987). Its unique distributional pattern was a reason that this is the only liverwort family mentioned in well-known Takhtadjan's (1978, 1986) "Floristic Regions of the World", provided there as an example of endemism in the Rocky Mountains floristic region. *Gyrothyra underwoodiana*, is easily recognized in the field when using a hand lens. While studying the liverwort flora in Bering Island (Commander Archipelago, Aleutian Island Arch) we immediately identified it when first encountered. Taking into account this species (and therefore family) was never recorded for the Russian liverwort flora, we draw attention to this interesting liverwort by extending its known distribution into the Commander Islands. We also provide new data on the distribution and ecology of this peculiar taxon.

Material and Methods

The material was collected in the course of exploration of the Bering Island liverwort flora in the summer of 2021, within the frame of the expedition supported by the Russian Foundation for Basic Research (see Acknowledgments section). The exploration covered previously unstudied sites in various parts of the island: northern, middle and southern. All collected specimens were delivered alive to the Laboratory of Cryptogamic Biota in the Botanical Garden-Institute in Vladivostok (herbarium VBGI), and studied microscopically using traditional methods of preparation. Photographs were taken through Olympus SZX16 and CX43 microscopes supplied with digital cameras ADF PRO 20 and ADF STD 15 respectively, installed with ADF image capture software.

Bering Island Vegetation and Climate

The environmental conditions of Bering Island were discussed in the bryological literature at least twice, by Bakalin (2005) and later by Fedosov *et al*. (2012). Therefore, only a brief summary is presented here. Commander Archipelago belongs to the westernmost Aleutians and contains two larger entities: Bering and Mednyi (= Copper) Islands and two small islets near northwestern part of Bering Island. The geomorphology of the Commanders is rather typical for the areas where two geological plates are contacted. The translated and slightly modified citation from Erlich and Melekestsev (1974: 327) is as following: "The Commanders represent two blocks raised on a shelf plate, forming the top of the ridge of the western part of the Aleutian Island Chain. Bering Island is located in the southwestern part of the plate, directly near the ledge of the continental slope, which breaks off to the trench". The island is expressed in the form of a ridge, the height of which ranges from 150 to 751 m a. s. l. in Steller Mt. (= Gora Stellera). Most of the island is occupied by terrigenous and terrigenous-volcanogenic deposits of the Paleogene-Lower Miocene age. Unlike other islands in the Aleutian chain there is no evidences of volcanic activity younger than Lower Miocene

time. The relief of most of the mountains is denudation-tectonic (Erlich, Melekestsev, 1974). Climate characteristics are determined by air mass circulation over northern part of the Pacific Ocean and cold-water currents from Arctic Ocean and a branch of the warm Kuroshio Current. The climate is mild with relatively warm winters and cool summers (Kursanova, Savchenko, 1966). A specific feature of island's rains is low intensity combined with a long duration (Mochalova, Yakubov, 2004). The mean air humidity is more than 80%, it changes little throughout the year (Kursanova, Savchenko, 1966). The snow cover plays important role in the distribution of vegetation. The snow cover average reaches thickness of 70–90 cm and accounts for about 40% of the annual precipitation. Resulting from the remarkable redistribution, the snow forms thick cover in narrow ravines and valleys where it reaches 10–15 m thick, although being almost completely blown away from the convex areas (Krestov, 2004).

The severe wind regime has a particular importance for the island vegetation formation. As noted by Kursanova and Savchenko (1966) average wind speed in Bering Island is 7.1 m/s (that is 3.5 times higher than, for instance, in Moscow). In each month it reaches hurricane force (40 m/s). Moreover, during the year this wind speed can be of any direction. There are 76 days per year (in average) when the wind speed average exceeds 15 m/s. The peculiar climatic conditions determined four main features of the island's vegetation: 1) absence of true forests; 2) the predominance of the tundra type vegetation in zonal habitats; 3) the predominance of swamp communities similar to those of Alaska, Chukotka, and northern part of the Kamchatka Territory; 4) the predominance of meadows and shrubs in drained areas of river valleys (Krestov, 2004). The tundra vegetation is the most common on the Commanders. It is represented by various variants of shrub, forb-shrub and scattered tundra communities developed over sedimentary gravel (Mochalova, Yakubov, 2004).

Unlike to the previous papers on the Commanders flora and vegetation, where the climate parameters were limited to the data obtained in the Nikol'skoye Weather Station new data was received within the last couple of years. The bioclimatic data for exact location (with of 30″ maximum resolution) is now possible (WorldClim, 2020–2022). Using cited data, we identified selected bioclimates for the collecting localities:

BIO1 = Annual Mean Temperature
BIO4 = Temperature Seasonality (standard deviation ×100)
BIO8 = Mean Temperature of Wettest Quarter
BIO9 = Mean Temperature of Driest Quarter
BIO10 = Mean Temperature of Warmest Quarter
BIO11 = Mean Temperature of Coldest Quarter
BIO12 = Annual Precipitation
BIO15 = Precipitation Seasonality (Coefficient of Variation)
BIO16 = Precipitation of Wettest Quarter
BIO17 = Precipitation of Driest Quarter
BIO18 = Precipitation of Warmest Quarter
BIO19 = Precipitation of Coldest Quarter

See Table 1 for the obtained data. For comparison purposes, we added the information on the same bioclimates for one collecting locality of *Gyrothyra* in British Columbia, where this genus is locally abundant (following to the map by Hong, 1987). The data on localities are from the list of specimens examined. For all coordinates, WGS 84 datum was used.

Table 1

The bioclimatic parameters for collecting localities

Locality	Northern part of Bering Island	Northern part of Bering Island	Middle part of Bering Island	Southern part of Bering Island	British Columbia
Latitude	55.28989°N	55.28594°N	55.06402°N	54.78589°N	48.5°N
Longitude	166.18599°E	166.19011°E	166.29661°E	166.57714°E	123.67°W
Specimen field ID	Com-161-3-21 [VBGI]	K-86-1-21 [VBGI]	K-118-21-21, K-118-25-21, Com-181-1-21 [VBGI]	K-128-5-21 [VBGI]	Schofield 187778 [UBC]
BIO1	1.25000	1.25000	1.10417	0.74583	8.32917
BIO4	604.50957	604.50957	664.96226	667.39132	526.91408
BIO8	3.80000	3.80000	3.23333	2.86667	2.80000
BIO9	1.61667	1.61667	1.81667	5.73333	14.86667
BIO10	9.26667	9.26667	9.80000	9.75000	15.13333
BIO11	-5.40000	-5.40000	-5.91667	-6.25000	2.33333
BIO12	785.00000	785.00000	846.00000	980.00000	1525.00000
BIO15	25.65195	25.65195	25.48722	25.91562	67.14912
BIO16	259.00000	259.00000	281.00000	332.00000	747.00000
BIO17	139.00000	139.00000	153.00000	181.00000	116.00000
BIO18	207.00000	207.00000	220.00000	254.00000	120.00000
BIO19	186.00000	186.00000	200.00000	237.00000	661.00000

To understand meteo-elements variation across the year we used climatic diagrams provided by Climate-data for Nikol'skoye Settlement (Nikol'skoye climate..., 2023). Unlike to the vast majority of sites in the Russian Far East mainland, the driest quarter is not the coldest one and warmest quarter is not the wettest. The driest quarter is from May to July, warmest — from July to September, wettest — from October to December and coldest — from January to March. According to the Table 1, the average annual temperature at collection localities in the north of the island is 1.25 °C, and in the south of the island 0.74 °C, the average temperature of the warmest quarter in the north is 9.26 and 9.75 °C in the south, the average temperature of the coldest quarter is –5.4 °C and –6.25 °C, respectively. The annual rainfall in the northern part is 785 mm, whereas in the southern part reaches 980 mm. The precipitation of warmest quarter (seems to be the only period in the island tundras when vegetation growth is possible)

varies from 207 mm in the northern part to 254 in southern part. It is worth mentioning, the climate characteristics provided by Kursanova and Savchenko (1966) based on the data from Nikol'skoye Settlement Weather Station are somewhat different: the average annual temperature there is 2.1 °C, and the annual rainfall is 470 mm only.

Results

Gyrothyra was collected in the northern, middle and southern portions of Bering Island. The species was found in abundance only in the southern part of the island. The following description is based on the Bering Island specimens cited below.

Gyrothyra underwoodiana M. Howe, 1897, Bull. Torrey Bot. Club, 24(4): 202–205, pl. 302–303. (Figs. 1–4, 5B)

Plants with mylioid or plagiochiloid habit in loose pure mats or mixed with *Nardia harae* Amakawa, prostrate to loosely ascending near apices, yellowish greenish to bright green, when well exposed sometimes with golden-brownish pigmentation in antical parts of upper leaves, rather soft, 1.5–3.0 mm wide and 10–15 mm long with older parts commonly decomposed, suppressed plants with gemmae production as small as 0.5 mm wide. Rhizoids rather rigid, abundant to rather dense, brownish-grayish, obliquely spreading, commonly united into loose fascicles, more densely produced in areas below the underleaves and arising from ellipsoidal purple pads on the ventral surface of the stem. Stem rather straight, yellowish greenish (like leaves in color), with exception of bright purple to purple black narrowly ellipsoidal pads along ventral side; branching postical lateral-intercalary, with some branch origins very postical adjacent to ventral merophytes that superficially resembles ventral branching; ventral segment of the stem 4–6 cells wide; between regularly spaced underleaves are narrow ellipsoidal, deep purple structures (pads) bear short connate rhizoids; stem cross section suborbicular, 300–550 μm in diam., outer cells smaller than inner cells, suborbicular, with slightly thickened walls and distinct, moderate to small in size concave trigones, 30–50 μm in diam., inner cells with obscurely thickened to rather thin walls, 5-polygonal to nearly orbicular in outline, 40–80 μm in diam., trigones small and concave; sections through ellipsoidal purple pads show short connate rhizoids with well-developed rhizoids in their marginal parts. Leaves succubous, contiguous to subimbricate, obliquely spreading to laterally appressed near shoot apex, dorsally alternate, somewhat interlocking, decurrent for ¼–⅓ of stem width, ventrally alternate to distinctly subopposite and commonly adjacent (but not connate) to underleaves on the both sides; leaf insertion from very oblique and subhorizontal in dorsal side to subtransverse in its middle and ventral sides, leaves generally concave, although the larger leaves have more or less convex antical third due to the insertion line suddenly curve as described above and then leaves acquire plagiochiloid look, in slide mounts nearly orbicular (larger) to ovate (smaller), varying from 1250 × 1300 to 2000 × 2500 μm, to 500 × 500 μm in small depauperate shoots; width is almost always larger than length, yet the leaves never look wider than long because of high position of the leaf base

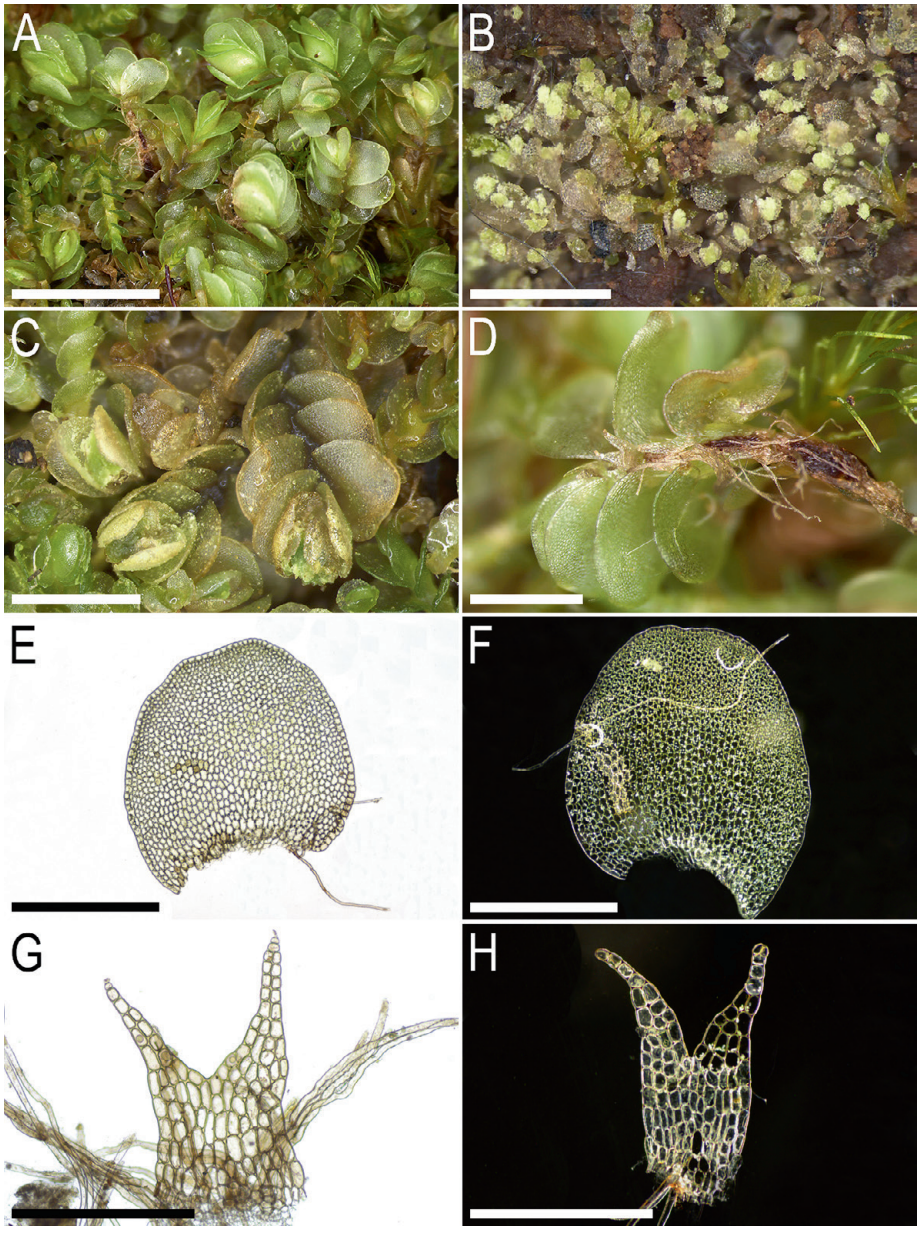


Fig. 1. *Gyrothyra underwoodiana* (A, D, F, H from *Bakalin, Klimova K-118-21-21*, VBGI; C, E, G from *Bakalin, Klimova K-118-25-21*, VBGI; B from *Bakalin, Klimova K-128-5-21*, VBGI). A — mat, dorsal view; B — mat, gemmiferous plants; C — shoots, dorsal view; D — shoot, ventral view; E, F — leaves (F – with dark field option); G, H — underleaves (H — with dark field option). Scales: 5 mm for A, B; 2 mm for C; 1 mm for D, E, F; 500 μm for G, H.

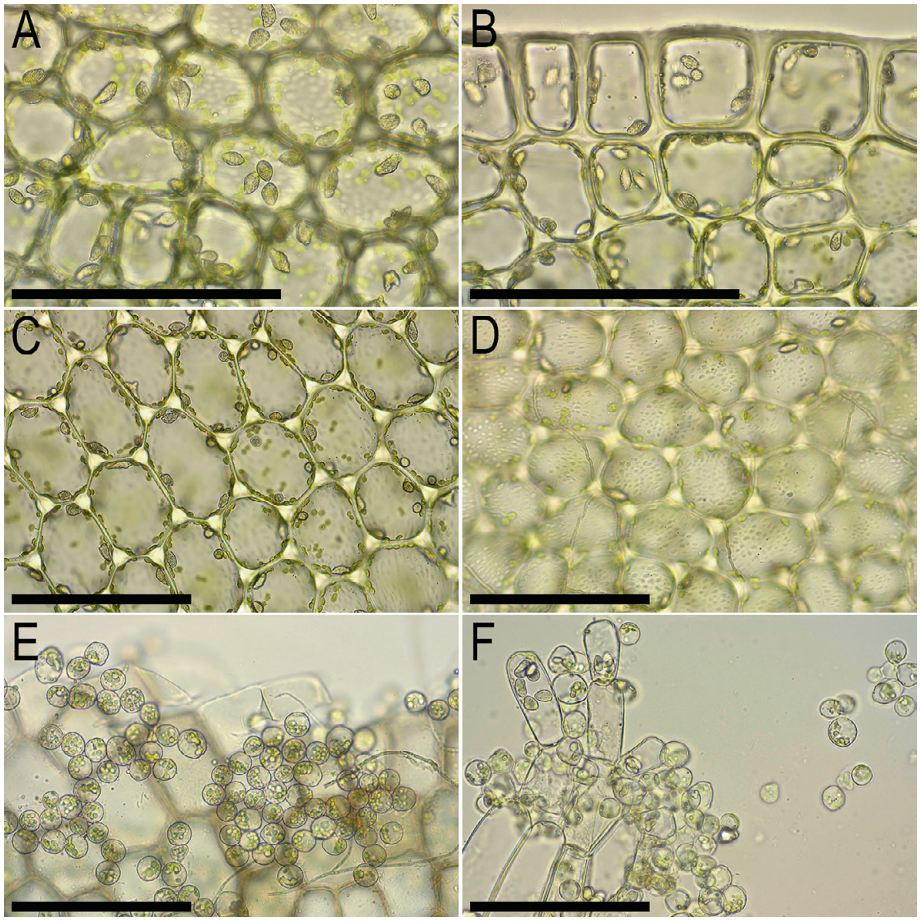


Fig. 2. *Gyrothyra underwoodiana* (A, B, D from *Bakalin, Klimova K-118-21-21*, VBGI; C, E from *Bakalin, Klimova K-118-25-21*, VBGI; F from *Bakalin, Klimova K-128-5-21*, VBGI). A — midleaf cells with oil bodies; B — leaf margin cells with oil bodies; C — trigones in midleaf cells; D — papillose cuticle of the midleaf cells; E, F — gemmiferous leaflet margins. Scales: 100 μm.

flanked by lateral sides extending below the leaf base. Underleaves regular, mostly hidden within rhizoids, obliquely spreading, smaller lanceolate, 620 × 750 × 175–230 μm, larger bilobed, 750–1000 × 300–550 μm, with subequal narrow lobes, divided by narrowly V-shaped sinus descending to ½–⅔ of the underleaf length; lobes straight or narrowly divaricate; lobes ending in 3–7 uniseriate cells. Cells in the midleaf oblong, mostly hexagonal, 40–75 × 35–50 μm, thin-walled; trigones moderate in size, convex; cells along margin swollen, bigger than adjacent intramarginal row, 26–50 μm along margin, forming distinct rim, walls thickened with moderate concave trigones; oil bodies 5–7 per cell, shortly fusiform to ellipsoidal, 7–10 × 4–6 μm; cuticle in the midleaf finely, but distinctly striolate, along margin narrowly striolate in outer row of cells and becoming verrucose inward. Gemmae 1-celled, greenish, 7–12 μm in diam., sparsely

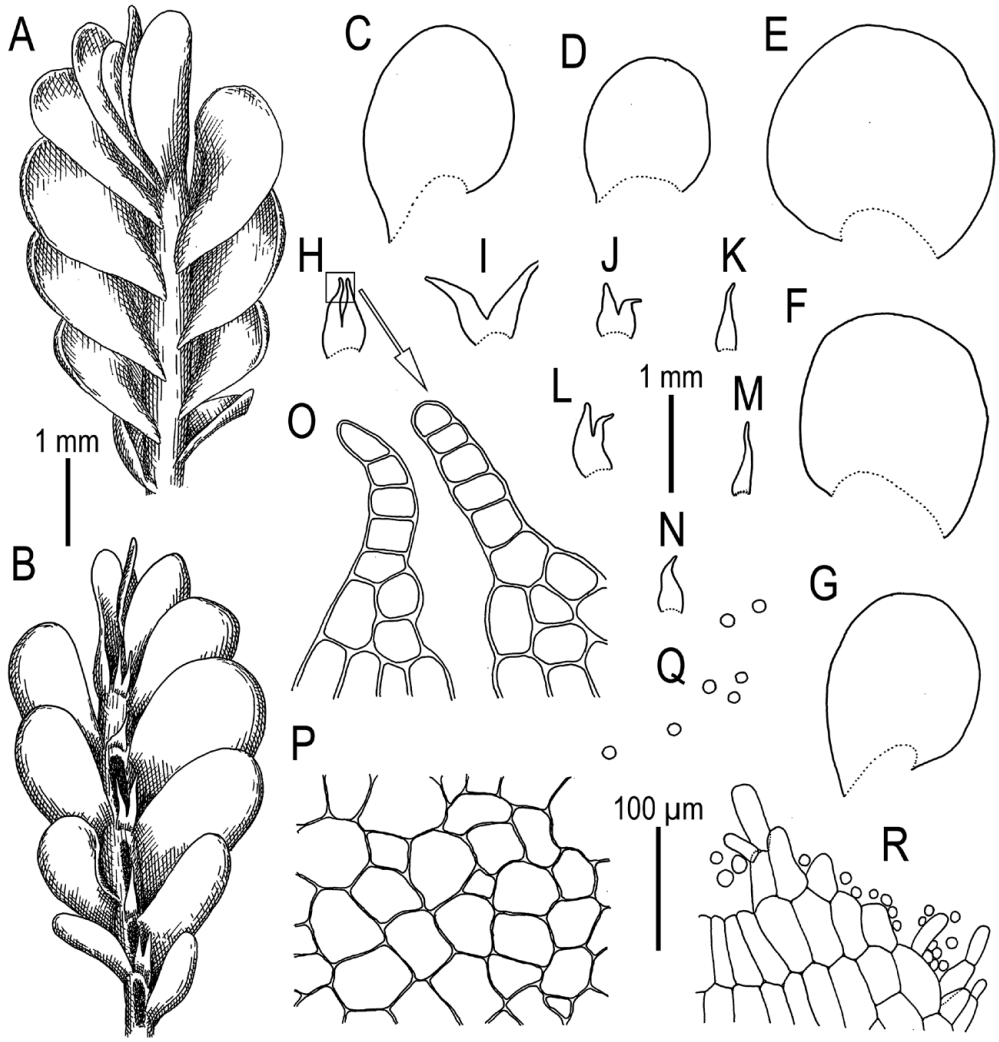


Fig. 3. *Gyrothyra underwoodiana* (*Bakalin, Klimova K-118-21-21*, VBGI).
A — shoot, fragment, dorsal view; B — shoot, fragment, ventral view; C–G — leaves; H–N — underleaves; O — cells in underleaf lobes, fragment of H; P — cells in underleaf middle part; Q — gemmae; R — gemmiferous leaf margin. Scales: 1 mm for A, B; 1 mm for C–N; 100 μm for O–R.

produced in well-developed shoots and nearly always present and usually abundant in small plants with distant leaves, produced in the shoot apex, from undeveloped, dentate leaflets hidden between normally developed leaves; gemmae production seems to stop further shoot development. [Gametangial shoots were not found in the studied specimens. The most recent description was provided by Crandall-Stotler (Gyrothyraceae..., 2022) as following: "Sexual condition, dioicous, with male plants more slender than females. Androecia intercalary on leading stems, with up to 6 antheridia

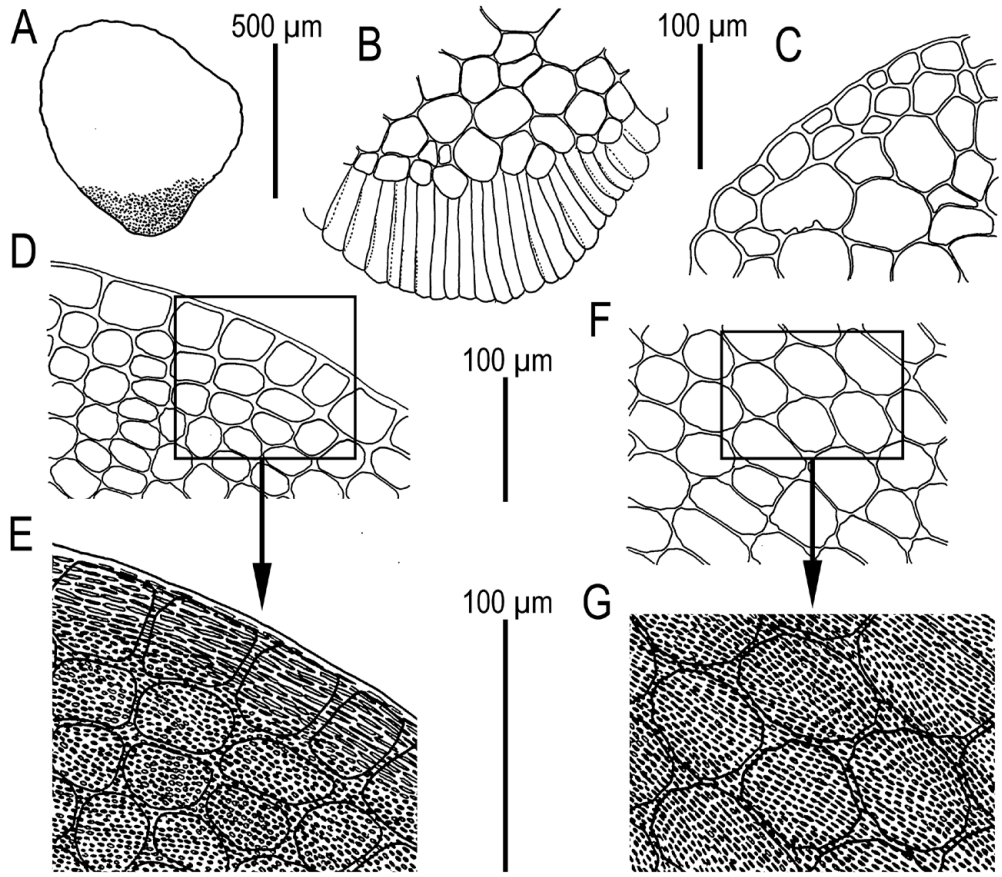


Fig. 4. *Gyrothyra underwoodiana* (*Bakalin, Klimova K-118-21-21*, VBGI).
A — stem cross section through zone with rhizoidal pad, general view; B — ellipsoidal, ventral pad with short connate rhizoids, cross-section, fragment of lower part; C — ellipsoidal structure, cross-section, fragment of upper part; D — leaf margin cells; E — papillose cuticle of marginal cells, fragment of D; F — midleaf cells; G — papillose cuticle of midleaf cells, fragment of F.
Scales: 500 µm for A; 100 µm for B–G.

per bract. Gynoecia subtended by 1–2 subfloral innovations; bracts and bracteoles in 2–3 series; perianth hyaline, tubular, only the constricted mouth emerging from the bracts, subtended by a well-developed fleshy, incipient marsupium. Sporophyte seta large, unspecialized. Capsule dark brown, ellipsoidal; capsule wall bistratose, without secondary wall thickenings; elaters free, with 2(–3) dark-brown spiral thickening bands; spores brown, spheroidal, apolar, with the wall minutely papillate"].

Specimens examined. **Russia**: Kamchatka Territory, Aleutsky District, Commander Islands, Bering Island, northeast part of the island, area about 1 km northeast of Sarannoe Lake, 55.28989°N, 166.18586°E, 106 m a. s. l., moist soil in part shade, 21 VIII 2021, *Klimova, Bakalin Com-161-3-21*;

ibid., 55.28594°N, 166.19011°E, 116 m a. s. l., road across hummocky tundra, partly shaded moist clayey soil in road cut, 21 VIII 2021, *Bakalin, Klimova K-86-1-21*; south part of the island, Bobrovaya River upper course, 54.78589°N, 166.57714°E, 52 m a. s. l., open moist clayey soil on slope to the river, 2 IX 2021, *Bakalin, Klimova K-118-21-21, K-118-25-21*, *ibid*., moist soil wall on riverside slope in part shade, 2 IX 2021, *Klimova, Bakalin Com-181-1-21*; middle part of the island, upper reaches of the left tributary of Myakishevskaya River, 55.06402°N, 166.29661°E, 263 m a. s. l., open moist clayey soil on slope to temporary stream, 7 IX 2021, *Bakalin , Klimova K-128-5-21* (all in VBGI). **Canada**: British Columbia, Vancouver Island, ca. 15 km S of Port Renfrew, 48.5°N, 123.67°W, 11 VII 2001, *W. B. Schofield 187778*; *ibid*., Stive Lake, 49.25°N, 121.7°W, 02 IX 1984, *W. B. Schofield 82675*; *ibid*., Chilliwack Mt., near summit, 49.15°N, 121.98°W, 10 III 2000, *W. B. Schofield, P. Woodsard 182056* (all in UBC).

Discussion

Morphological differentiation

Superficially, in the field, *Gyrothyra* may be mistaken for a strange *Mylia taylorii* (Hook.) Gray. The first feature that should alert the viewer is the gemmae distribution in masses between uppermost leaves present abundantly in some populations. Gemmae, although known, are very rare in *Mylia taylorii* in Pacific Asia. Unlike in Asia, in North America, as Schuster (1969: 1043) wrote for *M. taylorii* "asexual reproduction frequent, but not copious, by means of fasciculate gemmae arising from the margins of more or less ovate (never lanceolate) leaves with rounded apices". Therefore, even if gemmae are present, the distinctions are obvious because gemmae are never produced from the margin of normally developed leaves in *Gyrothyra*. The next 'candidate' for mistake is *Nardia geoscyphus* (De Not.) Lindb., that, however, has concave leaves, never with *Plagiochila*-like appearance with somewhat convex antical third of the leaf and never has the laterally appressed leaves near shoot apices, and never produces gemmae. Finally, *Gyrothyra* may be confused in the field with *Cryptocolea imbricata* R. M. Schust. due to similar shoot apices with somewhat laterally appressed leaves. However, sterile plants of *Cryptocolea* R. M. Schust. are much smaller (shoots never wider than 1.5 mm), golden-brownish, with leaves never *Plagiochila*-like and never with gemmae. All these confusions are possible only in the field, while under dissecting microscope, plants immediately differ from all three mentioned species in the presence of well-developed regular underleaves (present in *Nardia geoscyphus*, although much smaller and subulate, while commonly bifid and ca. ½ of leaf length in *Gyrothyra*) and the presence of narrowly ellipsoidal deep purple pads distributed singularly between underleaves and formed of short, densely connate rhizoids. Although most authors indicate only deeply bifid underleaves in *Gyrothyra*, this taxon also possesses narrowly triangular underleaves as drawn by Schuster (1955, fig. 1) and as observed in this study (Fig. 3K, M, N).

Even at the time of the original description there were no doubts that a new genus was in hand. Howe (1897) discussed the morphology of the taxon and stressed (l. c.: 204): "In respect to structure of the sporogonial envelopes, *Gyrothyra* is one of several very interesting transitions from the ordinary *Jungermannia* type to the

various pouch-bearing genera. Considered from this point of view and from certain other gametophytic characters, its nearest affinities are undoubtedly to be found in that section of *Nardia* represented by *Nardia haematosticta* Lindb. [= *N. geoscyphus*], of Europe. In manner of dehiscence of capsule it recalls the marsupiferous genus *Kantia* Lindb. [= *Calypogeia* Raddi]; but the valves of *Gyrothyra* are much longer and their cell-walls lack the local thickening, while, of course, no generic comparison of the two can be made so far as the gametophyte is concerned". Probably being befuddled by the similar to *Nardia* type of marsupium, Evans (1939) in his "Classification of the Hepaticae" placed *Gyrothyra* in the Jungermanniaceae. Likely, for similar reasons, Buch *et al.* (1938) placed *Gyrothyra* in the Epigonianthaceae and Müller (1940) in the Nardiaceae. The first researcher who argued *Gyrothyra* as the member of its own family was Schuster, who described Gyrothyraceae firstly invalidly (Schuster, 1951; no Latin diagnosis) and later legitimately validated it (Schuster, 1970). The main differentiation of the morphological features separating *Gyrothyra* from the other known liverwort families were formulated by Schuster (1951) and later in more pronounced form (Schuster, 1955: 139) cited here: "The most critical differentiating features of *Gyrothyra* are, as follows: 1. The bistratose valves devoid of thickenings (present in Jungermanniaceae and Ptilidiaceae). 2. The linear, spirally twisted valves (short, ovoid to elliptical, and straight in Jungermanniaceae and Ptilidiaceae, except for *Isotachis* Mitt.). 3. The 1:1 spore-elater diameter ratio (circa 4:1 in Ptilidiaceae, 2:1 in Jungermanniaceae). 4. The extreme anisophylly, with the underleaves deeply lobed, but the lateral leaves entire, at least eight times as large as underleaves (in Ptilidiaceae leaves nearly or quite isophyllous and all series of leaves nearly equally lobed; in Jungermanniaceae with no underleaves or with vestiges that are entire like the lateral leaves). 5. The longitudinal, usually purplish «cushioned» areas of the ventral merophytes situated between the underleaves that consist of small, specialized cells oriented at right angles to the leaf axis (i.e., in the same direction as the rhizoids), fused to form a spongy elevated tissue. The rhizoids almost all originate around the periphery of this region, from larger, relatively unspecialized cells, unpigmented like the rest of the stem cells. Ventral stem structure of this nature appears to be unique among the Hepaticae". The later methods of molecular systematics have confirmed the isolated position of *Gyrothyra* (Shaw *et al.*, 2015; Forrest *et al.*, 2006) as it was before argued based on the morphology (Schuster, 1951, 1955).

Ecology

On Bering Island, *Gyrothyra underwoodiana* is a species of habitats with disturbed vegetation cover. Most records were made from open to partially shaded moist soil (with various humification) along streams and small rivers (Fig. 5), although once the species was collected on a bank of small lake and once on a roadside across hummocky tundra (Fig. 6). A near constant companion of *Gyrothyra* is *Nardia harae* [= *Nardia scalaris* var. *harae* (Amakawa) Váňa] (Fig. 5B), a species of questionable status likely completely replaced in the Pacific Asia morphologically

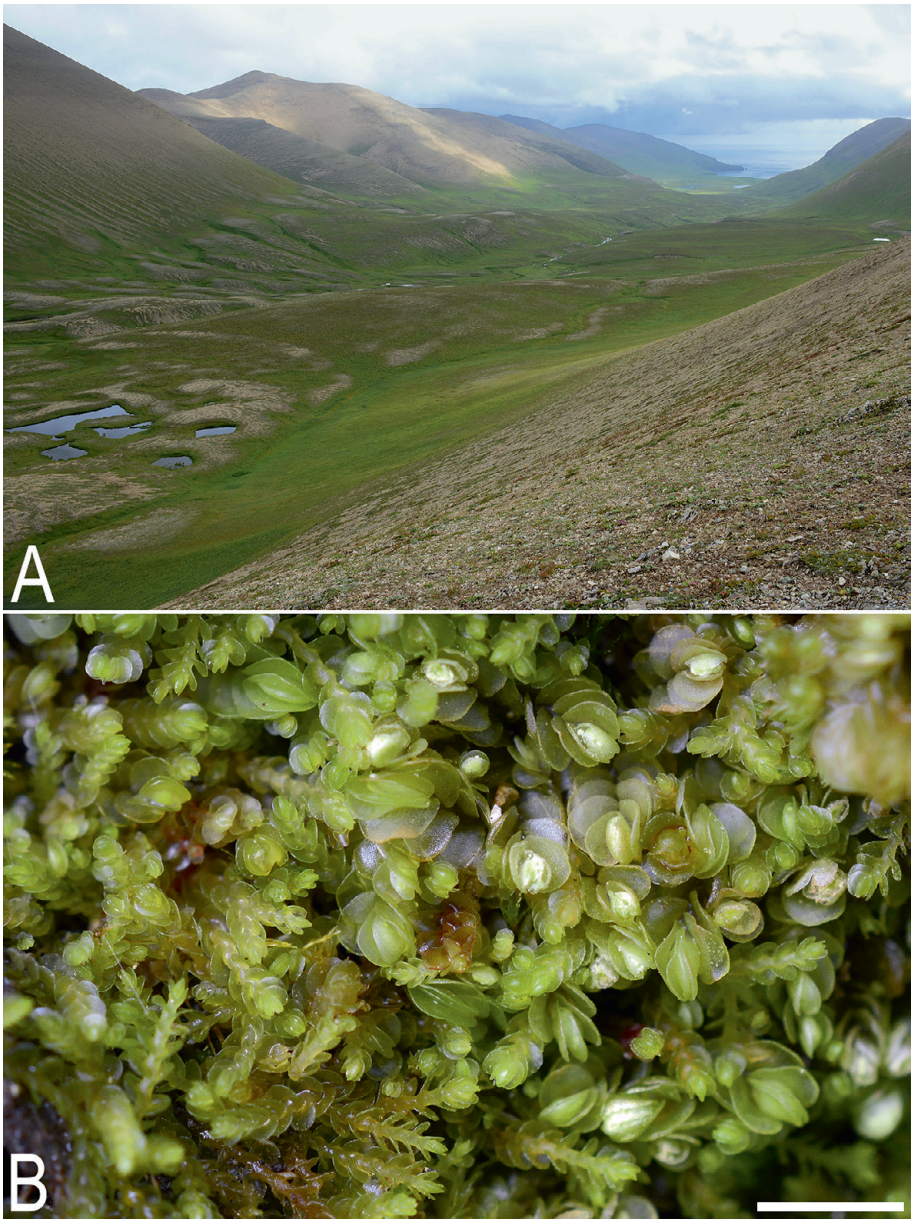


Fig. 5. A — Bobrovaya River valley: place of collection of *Gyrothyra underwoodiana* in the southern part of the Bering Island; B — mat of *Gyrothyra underwoodiana* mixed with *Nardia harae* in natural conditions (Bobrovaya River valley). Scale: 5 mm for B.
(Photos by K. G. Klimova, 2021).



Fig. 6. Place of collection of *Gyrothyra underwoodiana* in the north part of Bering Island. A — area about 1 km northeast of Sarannoe Lake, bank of small lake surrounded by hummocky tundra; B — *ibid*., road across hummocky tundra. (Photos by K. G. Klimova, 2021).

similar *N. scalaris* Gray. In broad scale, Bering Island is in the forestless zone where so common in northeast Asia except its northern extremes robust shrubs like *Alnus fruticosa* Rupr. and *Pinus pumila* (Pall.) Regel — are absent. The highest shrub in the Bering Island is *Salix alaxensis* (Andersson) Coville reaches 3.5 m high (Mochalova, Yakubov, 2004) although in the vast majority of cases the best developed individuals are 2 m high at maximum following to our observations.The short stature of the vegetation on the island is explained by strong winds and other climatic conditions. The vegetation itself is not composed predominantly of arctic elements. The vegetation of the Commanders is subarctic and in the absence of strong winds and low summer temperature, a taller vegetation would be developed in the Commanders. The vascular flora consists of many boreal elements that suggest its intermediate position between Hemiarctic and Boreal zones. Krestov (2004) provided a distributional analysis of vascular plant flora and formulated the following conclusions: 1) the flora is very similar and, probably, even belongs to the flora of the Kamchatka Peninsula; 2) the flora possesses more amphi-Pacific rather than boreal nature. Krestov (l. c.) also argued Commanders belong to the subarctic phytogeographic zone. At the same time, Mochalova and Yakubov (2004) judging from the dominant position of Asteraceae, Poaceae, and Cyperaceae argued the boreal nature of the vascular plant flora of the Commanders (cf. Yurtsev, 1968; Tolmachev, 1986). Therefore, although *Gyrothyra* was collected in completely forestless landscapes, its surroundings possess many boreal traits than would be expected from viewing the photographs of the tundra-like landscape.

The original description of the taxon (Howe, 1897: 203) provides data on ecology as "clay banks" and "earth in a brook". These notes show the species' habitat as being free of dense vegetation cover. This is indeed one of the most valuable characteristic of the taxon. The most recent, although brief, description of the habitat by Crandall-Stotler (Gyrothyraceae..., 2022) shows the same: "On shaded, moist bare soil, along roadsides, trails, or on damp rocks along small streams". Davison (1993) provides more definite data on the ecology of the taxon in the Aleutians. He stressed its frequent colonization of places with disturbed vegetation cover, including tire-tracks in grassy terrain. However, he noted (l. c.) that in the higher elevations the species tended to be distributed on soil along streams below melting snowbeds. The most recent mention of this species we were able to find is in the checklist of Attu Island liverworts (Talbot *et al*., 2018: 133) with description of its occurrence in "shaded ditch wall in tundra" that is similar to the description by Davison (1993). Therefore, the occurrence of *Gyrothyra* in forestless tundra or tundra-like communities is the natural trait of the species ecology in Aleutian Island Arch. Unlike the Aleutian occurrences, historical data (Howe, 1897) on the taxon's occurrence in coastal Pacific North America indicate coniferous forest zones. Moreover, within the forest zone the species seems to avoid the uppermost possible elevations and never occurs near the timberline. Even in California (Doyle, Stotler, 2006) where the species similarly occurs (l. c.: 157) "on shaded, moist bare soil of hillsides, and road and trail banks", the elevational range is 50 to 1200 m a. s. l.

Although all Californian reports of *Gyrothyra* are in the northern half of the state, these northern reports are not so cold as in Aleutians. Within California, the species is known from geographic regions of Klamat Ranges, North Coast and even inward of the continent to the Sierra Nevada. The dominate climate type in all those regions is Warm-summer Mediterranean (Beck *et al*., 2018), thus the same as mentioned above for the British Columbia occurrence of the species. The climate of Aleutians is classified by the ecoclimatic-phytogeographical system of Tuhkanen (1984, original not seen, cited after Talbot *et al*., 2018) as northern boreal, hyperoceanic, and perhumid. Unlike to the latter, the Köppen-Geiger climate classification cited above refers climate in the western Aleutians (westward of Unalaska) to Subpolar Oceanic Climate type. Therefore, being uniform in habitat preferences (the sites with disturbed vegetation in man-made habitats and along watercourses) the macroenvironmental characteristics changed drastically through the species range from tundra in Aleutians to the temperate forests in California.

The only associate of the species in Bering Island (present in the majority of vouchers) is *Nardia harae* — the species with questionable status and morphologically similar to *Nardia scalaris*. The associates in Aleutians (Davison, 1993) are more diverse and include in higher elevations (our comments are in square brackets): *Nardia japonica* Steph., *Scapania uliginosa* (Lindenb.) Dumort. [the identity may be questioned], *Schistochilopsis incisa* (Schrad.) Konstant. and *Moerckia blyttii* (Mørch) Brockm. In lower elevations *Gyrothyra* occurs together with *Nardia scalaris* Gray [rather referable to *N. harae*], *Scapania scandica* (Arnell et H. Buch) Macvicar [rather referable to *S. parvifolia* Warnst.], *Solenostoma obovatum* (Nees) C. Massal. [rather referable to *S. subellipticum* (Lindb. ex Heeg) R. M. Schust.] *Solenostoma rubrum* (Gottsche ex Underw.) R. M. Schust., *Pellia neesiana* (Gottsche) Limpr., *Diplophyllum obtusifolium* (Hook.) Dumort. [rather referable to *D. sibiricum* Vilnet et Bakalin], *Fuscocephaloziopsis pleniceps* (Austin) Váňa et L. Söderstr. and *Calypogeia muelleriana* (Schiffn.) Müll. Frib. *Gyrothyra* seems to be an easily spreading species. Davison (1993) indicated for Aleutian plants of *Gyrothyra* the frequent presence of sporophytes and gemmae, whereas in Bering Island, we were able to find only gemmae. The gemmae, however, are sometimes produced in masses and should be easily disseminated by water flow along streams and vehicle wheels, and man and animal legs along the roadsides.

The better developed populations are observed in the southern part of the island and survive in much colder and wetter conditions than it would follow from the data provided by the Weather Station in northern part of the island. The comparison of climates in Bering Island with data for the bioclimates in one locality of *Gyrothyra* in British Columbia where the species is the most abundant (following to the map by Hong, 1987) shows: 1) mean annual temperature in British Columbia locality is much higher and reaches 8.33 °C, 2) annual precipitation is twice higher than in the northern part of Bering Island and reaches 1525 mm per year, 3) however, the precipitation of the warmest quarter is even lower than in northern part of Bering Island and reaches only 120 mm, 4) mean temperature of driest quarter reaches 14.9 °C versus

1.6 °C in the northern part of Bering Island and 5.7 °C in its southern part; 5) the temperature of the wettest quarter in British Columbia is the same as in southern part of Bering Island (2.8 °C) and lower than in northern part of the Island (3.8 °C). Several discrepancies actually arise from the fact the wettest quarter in Bering Island (October-December, see above) is not the coldest, while in British Columbia it is nearly corresponding to the coldest quarter of the year. The general climate characteristics are different in British Columbia locality, where the climate is warm-summer Mediterranean, while in Bering Island it is Subpolar Oceanic Climate (Beck *et al*., 2018).

Distribution

Howe (1897) described *Gyrothyra underwoodiana* based on the specimens collected in Humboldt County of California State of the U.S.A. and Burrard Inlet of British Columbia in Canada. For a long time, this species was known mostly between these two points. Hong (1987) summarized the distribution of the taxon in the map (Fig. 5 in l. c.), where the area is stretching from southern tips of Pacific Alaska mainland via British Columbia, Washington, Oregon and to the middle California. Taking into account that this species occurs from low to middle elevation, the community types are somewhat vary along latitudinal gradient, although always belong to the Temperate Coniferous Forests zone (Olson *et al*., 2004). Davison (1993) was the first to document the occurrence of this species through the Aleutian Island Arch to the Near Islands (Attu) and mapped its distribution (Map 27 in the l. c.). The distribution of *Gyrothyra* in Aleutians is confined to forestless landscapes cited as tundra by Davison (1993).

Efforts to find *Gyrothyra underwoodiana* in Russia have been underway for over 20 years starting from the first visit of Bering Island by the author Bakalin in the summer of 2002. Having been unsuccessful he asked the late Dr. W. B. Schofield (UBC) for any tips to aid the field search and for his opinion on the possibility to find either *Gyrothyra underwoodiana* or *Takakia* S. Hatt. et Inoue in Russia. He answered 20 years ago and suggested that it looks to be difficult to find both genera in Commander Islands because even in the Near Islands of the Aleutians (Attu Island, the most close to Commanders) these taxa occur mostly in man-made habitats, thus were probably introduced to these islands. Similar concerns are provided by Davison (1993: 178) who firstly recorded *Gyrothyra* from Aleutians: "Given its widespread occurrence in the Aleutians and its distinctive morphology, it seems unlikely though not impossible that *Gyrothyra underwoodiana* was overlooked by many of earlier collectors. Indeed, *Gyrothyra* having an affinity for disturbed habitats may be an adventive species in the Aleutians, having arrived with shipments of heavy equipment employed since World War II, which locally create major disturbances across the tundra. From these initial introductions *Gyrothyra* may have then spread to the naturally disturbed tundra sites it presently occupies".

Taking into account that Alaska, including Aleutians (except for the Commanders) was sold by the Russian Empire to the United Stated in 1867 and since then nearly all transportation between Commanders and other Aleutians was ended, it was one

would hardly to expect these taxa would be found in Bering Island in roadsides, because all now existing roads are newly constructed in the island post-1950. Therefore, if the 'introduction' model of the Aleutian distribution is adopted, the introduction event to the Commanders would have occurred long before the World War II. An opposite possibility is the natural occurrence of *Gyrothyra* in the Aleutian tundras before industrialized human activity and the species then locally spread to roadsides. There could be two reasons for the natural spreading of the species to the Bering Island from the Aleutians. Firstly, these are winds, which, as mentioned above, often reach hurricane speed. In addition, easterly winds absolutely dominate the Aleutians, as the example of Adak Island (WeatherFlow Inc., 2023) shows. Secondly, it is the possibility of the introduction by birds. Bering Island has long been shown to be the site of occurrence for both Palearctic and American bird species (Stejneger, 1885), which move between islands in search of couples and can theoretically distribute gemmae and spores. In addition, some migratory birds travel along the Aleutian Chain and can transfer propagules to the nearest islands too (Aleutian Canada Goose ..., 2023; Gibson, 1981).

Among six specimens collected in Bering Island, the only one was found in the roadside in the only populated part of the Bering Island. Other specimens were collected in the areas with disturbed vegetation cover, where cover was disturbed due to natural forces of riverside denudation and where no roads exist.

Conclusion

The Aleutians, as the island chain connecting Asia and America across the Pacific Ocean, are an admirable place of interpenetration of Asian and American floras in various taxonomic divisions, including liverworts. There is the somewhat admitted consensus that the imaginary Tatewaki phytogeographic line going between Commanders and Near islands (Attu and Agattu) is the serious phytogeographic border between Asian and American floras of vascular plants (Tatewaki, 1963), liverworts (Bakalin, 2009) and mosses (Fedosov *et al*., 2012). However, as it likely should be, the distribution of a few species does not easily fit into the Procrustean bed of this regularity; the occurrence of *Gyrothyra underwoodiana* in Bering Island is an exception to the common rule. Phytogeographically this record seems to fall within the pattern of distribution set by a series of mosses, e. g., *Brachythecium frigidum* (Müll. Hal.) Besch., *Claopodium bolanderi* Best, *Lescuraea baileyi* (Best et Grout) E. Lawton and *L. saviana* (De Not.) E. Lawton, etc. (Fedosov *et al*., 2012) easily crossing Tatewaki line to access the Commanders. Moreover, it is unknown whether the distribution of this taxon in the Aleutians is natural phenomenon or rather the result of introduction of invasive species due to human activity. In any way, it is probable to predict that this find is not the last in a series of discoveries of penetration of Western American species to the West.

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