Liverworts from Attu Island, Near Islands, Aleutian Islands, Alaska (USA) with comparison to the Commander Islands (Russia)

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ABSTRACT

The liverwort flora of Attu Island, the westernmost Aleutian Island in the United States, was studied to assess species diversity in the hyperoceanic sector of the northern boreal subzone. The field study was undertaken in sites selected to represent a spectrum of environmental variation, primarily within the eastern part of the island. Data were analyzed using our own collections on Attu Island, supplemented with information from published reports to compare bryophyte distribution patterns at three levels, the Northern Hemisphere, North America, the Commander Islands of Russia, and Alaska. A total of 112 liverworts were identified and a substantial number, 34 species (30%), were new reports from Attu Island and one was new to Alaska. Geographic elements dominating the flora included arctomontane (26%), arctoboreomontane (23%), montane (20%), and boreal (14%) species, while arctic species were almost absent (1%). The liverworts of the Attu Island-Commander Islands region were widespread species with over 70% circumpolar, or nearly circumpolar; nevertheless large gaps were present in some of their distributions with a floristic depression in liverwort distribution between Attu and the Commander Islands.

Keywords: Hepaticae, phytogeography, northern boreal, hyperoceanic, Bering Land Bridge

РЕЗЮМЕ

Тэлбот С.С., Схофильд В.Б., Ванья И., Тэлбот С.А. Печеночники острова Атту, Ближние острова, Алеуты, Аляска (США) в сравнении с печеночниками Командорских островов (Россия). Представлены результаты исследований флоры печеночников острова Атту, самого западного алеутского острова в США, на основании которых проведена оценка видового разнообразия печеночников в гиперокеаническом секторе северной подзоны бореальной зоны. Полевые работы проводились на участках, отражающих спектр изменений условий окружающей среды, прежде всего в восточной части острова. В анализ включены наши собственные коллекции с острова Атту и опубликованные данные других авторов. Проведен анализ распределения печеночников на трех уровнях: в Северном полушарии, в Северной Америке, на российских Командорских островах и на Аляске. Было выявлено в общей сложности 112 видов печеночников, значительная часть которых – 34 вида (30 %) – впервые отмечены на острове Атту, а один вид является новым для Аляски. Географический анализ флоры позволил установить, что в спектре географических элементов преобладают арктомонтанные (26 %), арктобореомонтанные (23 %), монтанные (20 %) и бореальные (14 %) виды, в то время как арктические виды почти отсутствуют (1%). Печеночники, совместно встречающиеся на острове Атту и Командорских островах, на 70 % представлены циркумполярными или почти циркумполярными видами; тем не менее, существуют большие различия между флорами печеночников Атту и Командорских островов.

Ключевые слова: Неритисае, фитогеография, бореальная зона, гиперокеанический климат, Берингский мост суши

Переведено редколлегией

INTRODUCTION

From the northwestern portion of the North America landmass, the Aleutian Island Archipelago extends in an arc 1900 km into the northern Pacific Ocean from Unimak Island – the easternmost island – through Attu Island, the westernmost island in the United States, toward the Commander Islands of Russia, which comprise the westernmost

portion of the archipelago. These windswept, often foggy volcanic islands are of considerable phytogeographic interest because they occur along the southern margin of the Bering Land Bridge and function as an important region for plant dispersal between Asia and North America (Elias & Crocker 2008). Species dispersal occurs in at least two directions, westward from North America along the Aleutian Archipelago, and eastward from Asia toward mainland

Alaska and the more temperate North Pacific Coast. Attu Island is of particular interest because of its relatively close proximity (ca. 300 km) to the Commander Islands of Russian Aleutian Islands. Hultén (1960) indicated the Aleutian Islands belong to the same floral and vegetational province as the Kamchatka Peninsula of Russia with the strongest vascular plant relationships occurring in the westernmost islands of Attu, Agattu and Alaid. Of the approximately 530 vascular plant species comprising the Aleutian vascular flora, 70 % occur in both Alaska and Kamchatka. Attu Island falls within the boundary of the U.S. Department of Interior's (DOI) Alaska Maritime National Wildlife Refuge.

The Aleutian Archipelago is among the most dynamic ecosystems on Earth, due in part to periodic volcanic eruptions that can eradicate island floras via thick ash deposits (e.g., Talbot et al. 2010). Liverworts are often among the first terrestrial plant species to recolonize perturbed landscapes (Smith & Griggs 1932), and are known to deliver mycorrhizal inoculum and improve the establishment of vascular plants (Jongmans et al. 2001, Kowal et al. 2016). The biodiversity of liverworts in the Aleutian Archipelago is not well known (Söderström et al. 2015). The primary objectives of this study are to, 1) establish a checklist of the liverwort flora of Attu Island, based on our collections and the collections of other researchers; 2) assign a commonness rating – abundant, common, uncommon, and rare – for each species; 3) record habitat information of each species; and 4) collect voucher specimens of liverwort species. Secondary objectives were to 5) describe the phyto-geographic pattern of Attu liverworts with liverwort distribution in circumpolar regions to provide a comparative context, including comparing the liverwort flora of Attu with that of the Commander Islands. The list also provides baseline data for detecting floristic shifts due to impacts of

climate change, including generally predicted warming air and ocean temperatures and accompanying changes in precipitation, as well as synergistic interactions among specific factors characteristic of oceanic islands (Harter et al. 2015), including here the impact of ash on floras due to periodic volcanic activity characterizing the Aleutian Archipelago (Anderson & Bank 1952, Heusser 1990). This research thus informs the DOI regarding biodiversity on lands that the bureau manages. Because the Commander Islands fall within the Commander Islands Biosphere Reserve and is administered by the Ministry of Natural Resources of the Russian Federation, this research provides the Ministry with valuable comparative biodiversity data as well.

A total of 267 liverwort species are reported for Alaska, excluding the Aleutian Islands, but given the relatively poor historical focus on Alaska liverworts and despite their ecological significance and the richness of the Alaska landscape, it is likely a number of new records are yet to be reported (Söderström et al. 2015). Liverwort collections are reported from Attu Island by Clark & Frye (1948, 1949), Davison (1993), Evans (1900), Frye & Clark (1946), Hong (1980), Konstantinova & Mamontov (2010), Macoun (1902), Persson (1952, 1968) and Sharp & Hattori (1968). In total these reports list approximately 84 species for Attu Island (Davison 1993).

STUDY AREA

The Aleutian Islands are composed of a chain of sedimentary islands, eroded from older volcanic formations, and capped by steep volcanoes (Gallant et al. 1995). Attu Island is located in the westernmost Aleutian Islands governed by the United States, at approximately 52.83°N, 173.18°E (Fig. 1); Attu Island was extensively glaciated during late Quaternary time, probably during the Wisconsin

Figure 1 Location of Attu Island, Alaska, and map of the liverwort collection sites. Circled numbers (1 – 28) are collection sites and listed in the Methods section

sinan Stage (Gates et al. 1971). The Commander Islands of Russia form a part of the Aleutian Islands with Bering Island (55.02°N, 165.98°E) and neighboring Copper Island. The geosystems of Bering Island may be divided into three types: plain, mountain and coastal (Ivanov 2003); this classification may be similarly applied to Attu Island. Based on geological evidence (Tsvetkov et al. 2010), the Commander Islands are older than more eastern islands of the Aleutian Archipelago; evidence of volcanism in the Commander Islands are dated to the Miocene.

A maritime climate prevails throughout the region. The ecoclimatic-phytogeographical system of Tuhkanen (1984) characterizes the Aleutian Islands as northern boreal, hyperoceanic, and perhumid. Mean annual temperature and precipitation of Attu are 3.8°C and 1341 mm, respectively (Fig. 2). An alternative climatic classification, Patric & Black (1968) classify the climate of the Aleutian Islands according to Thornthwaite's system (Thornthwaite 1948) as AC'2rc', that is perhumid, warm microthermal, no season of rainfall deficit, temperature efficiency normal to warm microthermal. A multivariate analysis of climate along the southern coast of Alaska by Farr & Hard (1987) indicate the Aleutian Islands form a distinct coastal climatic group with moderately cool temperatures in the fall, winter and spring and much colder summers than other coastal stations. In terms of oceanity, Attu is relatively more hyperoceanic (O_3) than Bering (O_2 ; Tuhkanen 1984).

General accounts of the vascular flora and vegetation of the Aleutian Islands are provided among others by Bank (1951), Gallant et al (1995), Hultén (1960, 1968), and Tatewaki & Kobayashi (1934). Information on the vegetation of Attu Island is rather limited; Heusser (1990) published on the late Quaternary vegetation and Talbot & Talbot (1994) described the coastal vegetation with quantitative comparisons to Aleutian vegetation types described by others. The comparison pointed to a close relationship to the beach and beach-meadow types of the Aleutian Islands and Kamchatka. In a similar manner Krestov (2004) compared the vegetation of the Commander Islands to Attu Island, and other Aleutian Islands and Beringian locations. As stated by Krestov et al. (2010) the archipelagos of the Aleutian, Kuril and Japanese Islands are typified by the presence of plant communities derived from the pre-Pleistocene humid Beringian vegetation complex, which was named Hultenia by Tatewaki (1963).

A factor of major importance in the Aleutians is volcanism as indicated by the thickness, distribution and frequency of tephra layers numbering five on Attu. These recurrent volcanic eruptions with widespread accompanying ash falls influence vegetation composition and distribution (Heusser 1990).

METHODS

Collections were made by Sandra Looman Talbot (SLT), Stephen S. Talbot (SST) and Wil-

fred B. Schofield (WBS) during four periods: 1) July-August 1988 (SLT and SST), 2) August 2000 (SLT, SST, & WBS), 3) September 2002 (SST & WBS) and 4) August 2003 (SST). All specimens are vouchered at UBC with partial sets deposited at DUKE and PRC.

Major collection sites are shown in Fig. 1, and are listed below by site number (1–28) followed by a general geographic descriptive name, latitude, longitude, and elevation.

1. Abraham Bay, 52°53'N, 172°47'E; 5 m;
2. Alexai Point, 52°51'N, 173°14'E; 195 m;
3. Beach Road, 52°50'N, 173°09'E; 5 m;
4. Cape Wrangell, 52°56'N, 172°27'E; 195–488 m;
5. Casco Point, 52°49'N, 173°10'E; 5 m;
6. Chirikof Point, 52°51'N, 173°24'E; 6 m;
7. Coast Artillery Hill, 52°51'N, 173°10'E; 122–152 m;
8. Gilbert Ridge, 52°51'N, 173°14'E; 30–122 m;
9. Holtz Bay, West Arm, 52°55'N, 173°07'E; 12 m;
10. Jarmin Pass, 52°58'N, 173°08'E; 213–610 m;
11. Jim Fish Creek, 52°54'N, 173°14'E; 61 m;
12. Kingfisher Creek, 52°49'N, 172°09'E; 30–100 m;
13. Lake Elwood, 52°52'N, 173°10'E; 12 m;
14. Murder Point, 52°48'N, 173°10'E; 10–30 m;
15. Nevidiskov Creek (West Arm Nevidiskov Bay), 52°48'N, 172°48'E; 244–457 m;
16. O'Donnell Valley, 52°54'N, 173°08'E; 20–30 m;
17. Peaceful Valley, 52°50'N, 173°08'E; 30–46 m;
18. Robinson Ridge, 52°53'N, 173°09'E; 396–405 m;
19. Sarana Bay, 52°51'N, 173°23'E; 11 m;
20. Siddens Valley, 52°52'N, 173°14'E; ca 10–30 m;
21. Sonam Beach, 52°48'N, 173°06'E; 15 m;
22. Temnac Valley, 52°50'N, 173°03'E; 6–472 m;
23. Terrible Mountain, 52°51'N, 173°09'E; 61–273 m;
24. Thirty-Seven Hill, 52°50'N, 173°09'E; 50–189 m;
25. USCG Loran A Station, 52°50'N, 173°10'E; 10–30 m;
26. USCG Loran C Station, 52°50'N, 173°04'E; 20–50 m;
27. West Mountains, 52°49'N, 173°08'E; 50–579 m;
28. West Massacre Valley (Henderson River), 52°50'N, 172°50'E; 20–60 m.

Figure 2 Climate diagrams for Attu Island, Alaska, and Nikolskoye, Bering Island, Russia. Abscissa shows the months January to December. Ordinate: the first dash-mark upwards represents 10°C and 20 mm, respectively. Name of station given in upper left-hand corner with latitude/longitude and elevation given below. Number of years data were collected for temperature and precipitation given in brackets, followed by mean annual temperature and mean annual precipitation. Top curve is mean monthly precipitation and lower curve is mean monthly temperature. Climate diagram prepared using Lieth et al (1999) based on data Leslie (1989)

We sought to collect from a spectrum of habitats from seashore to mountain summits (Fig. 3); these habitats included rocky and sandy shores, beach meadows and dunes, mesic forb and graminoid meadows, fern meadows, dwarf shrub heaths, alpine fellfields, mires, ponds and streams, snowbeds, rock cliffs and crevices. For each species we estimated commonness using the classes of Hickman (1993): (1) abundant; very likely to be encountered; nearly always found in appropriate habitats, sometimes forming dense stands; (2) common; likely to be encountered; (3) uncommon; unlikely to be encountered and sometimes not present in appropriate habitats; and (4) rare; extremely unlikely to be encountered, often not present in appropriate habitats, and often restricted to a small number of sites.

The commonness class is followed by habitat information. In turn these data are followed by collection numbers; those numbers starting with the alpha letters “AT” are those of SST and SLT, while all others are those of WBS. Literature citations are given for each species previously reported in the Aleutian Island. Site location names follow. Species reported for the Commander Islands are then given with a literature citation(s).

To assess hepatic distribution within the North Holarctic we assigned the categories of Konstantinova (2000) to each species: I. Arctic: a. Circumpolar, b. Subcircumpolar, c. East Siberian-American-Groenlandic, d. Siberian-American, e. Siberian-West American, f. Chukchi-American-Groenlandic, g. West American, h. Unclear areal; II. Arctomontane: a. Circumpolar, b. Subcircumpolar, c. Amphioceanic, d. Disjunctive, e. Euro-Siberian, f. Eurasian-Groenlandic, g. Eurasian-Groenlandic-West American, h. Eurasian-West American, k. Siberian-West American, l. Unclear areal; III. Montane: a. Circumpolar, b. Subcircumpolar, c. Amphioceanic, d. Subatlantic, e. Pacific, f. Disjunctive, g. Euro-West American, h. Euro-Groenlandic, i. American-Groenlandic, k. European, l. Unclear areal; IV. Arctoboreomontane: a. Circumpolar, b. Subcircumpolar, c. Amphioceanic, d. Disjunctive e. Unclear areal; V. Boreal: a. Circumpolar, b. Subcircumpolar, c. Subatlantic, d. European, e. Euro-American, f. Euro-Groenlandic, g. Disjunctive; VI. Temperate: a. Circumpolar, b. Amphioceanic, c. Pacific, d. Euro-American, e. Eurasian, f. European, g. Unclear areal; VII. Cosmopolitan; and VIII. Unclear distribution. Unassigned species were assigned a category using Bakalin (2010a) and Damsholt (2002).

With the exception of species determined by WBS, for which no indication is given, the determiner's name is indicated by initials, which follows the collection number(s): BS (Blanka Shaw), PD (Paul Davison), Kathrin Feldberg (KF), Olivia Lee (OL) and Jiří Váňa (JV).

Complete information, including detailed collection site descriptions, site locations, latitudes, longitudes, elevations, habitat, collection date, quadrangle map, and determiners, are available at UBC.

RESULTS

Annotated catalog of liverworts

In the following checklist, species reported from Attu are arranged in alphabetical order. Bryophyte nomenclature follows Söderström et al. (2016) for liverworts. An asterisk indi-

cates a species newly reported for Attu Island, two asterisks indicate species new to the Aleutian Islands, and three asterisks indicate species new to Alaska. Each species is followed by a series of descriptors: synonyms [in brackets], commonness, habitat, collection number, collection site, previous reports documenting presence on Attu, and geographical distribution, including in some cases distribution elsewhere.

We list 112 liverworts from Attu Island. The number of Attu Island liverwort species equals that of the Commander Islands, where approximately 112 species are reported (Bakalin 2010a). Thirty-four liverwort species (30 % of the Attu flora) are newly reported for Attu and one, *Herbertus delavayi*, is new to the Aleutian Islands and Alaska. Approximately 66 liverwort species occur in both the Commander Islands and Attu Island; the Attu flora includes 40 species (58 %) that occur on both Bering and Attu Islands.

Acrobolbus ciliatus (Mitt.) Schiffn.

Rare; shaded wall, humus hole in gully, 116047A (mixed with *Diplophyllum taxifolium*) (BS); reported by Sharp & Hattori (1968); Schofield (2002) noted this species is confined to Alaska to two localities: Baranof Island in southeast Alaska and Attu Island in the Aleutians; Peaceful Valley; IIe.

Anastrepta orcadensis (Hook.) Schiffn.

Rare; side of humus hole on slope, sedge wetland; 115667 (mixed with *Diplophyllum albicans*) (BS), 115992 (BS); reported by Persson (1946); Lake Elwood, Terrible Mountain; This species is confined to humid areas near the coast in the Aleutians, southeast Alaska, and neighboring British Columbia (Schofield 2002). IIIf.

Aneura pinguis (L.) Dumort.

Uncommon; damp cliff on humus; AT225, 115569, 116335, 120246; reported by Clark & Frye (1948); Casco Point, Murder Point, Thirty-Seven Hill; Bering Island (Bakalin 2005); VII (bipolar).

Anthelia julacea (L.) Dumort.

Abundant; seepage slope near outcrop, wet late snow patch area; AT 26-27, 115257, 115491A, 115516, 115777, 115816, 115954, 120169, 120394; Davison (1993) reported a specimen collected by Sharp 9023; Beach Road, Casco Point, Coast Artillery Hill, Massacre Bay, Robinson Ridge, Terrible Mountain, Thirty-Seven Hill; Bering Island (Bakalin 2005); IIb.

**Anthelia juratzkana* (Limpr.) Trevis.

Abundant; dryish tundra crusts; fellfield; AT 385, AT 88-889, AT18-41, AT26-24, AT27-34, 115516; Cape Wrangell, Jarmin Pass, Robinson Ridge, Thirty-Seven Hill, West Mountains; Bering Island (Bakalin 2005); IIa.

Barbilophozia barbata (Schmidel ex Schreb.) Loeske [*Lophozia barbata* (Schmidel) Dumort.]

Reported by Persson (1952); IVa (bipolar).

Barbilophozia lycopodioides (Wallr.) Loeske [*Lophozia lycopodioides* (Wallr.) Cogn.]

Rare; Nootka lupine meadow, crowberry heath, bank of streamlet, fellfield at mountain summit, Fleabane meadow, open area near road; AT48-49, AT49-36, AT62-41, AT64-38, AT88-756, 116292 (BS), 120122, 120384; reported by Clark & Frye (1948); Murder Point, Peaceful Valley, Robinson Ridge, Terrible Mountain; Bering Island (Bakalin 2005); IVa.

**Barbilophozia sudetica* (Nees ex Huebener) L. Söderstr., De Roo et Hedd. [*Lophozia sudetica* (Nees ex Huebener) Grolle]

Common; dark strands overgrowing *Sphagnum* in tundra, *Sphagnum* at edge of pond base of terrace bank, bank of

Figure 3 Major habitat types of Attu Island: A – view from eastern Attu Island of the snowbed-rich Attu Mountain area, 18.09.2002. Convex ridge landforms are dominated by dwarf-shrubs and concave depressions are dominated by graminoid and forb meadows. B – view from a fellfield on Gilbert Ridge, Attu Island, looking southeast along West Massacre Valley toward Massacre Bay, 18.09.2002. Terrible Mountain (elevation ca. 610 m) is on the right with Coast Artillery Hill (elevation 168 m) and Lake Elwood in the distance. The valley plain is dominated by mires of Lyngbye sedges and tall cottongrass. C – view southwest from Peaceful River toward Kingfisher Creek in the Weston Mountains (elevation ca 488 m), Attu Island, Alaska, 13.09.2002. Forb meadows dominate riparian sites and sedge mires occupy the toe slopes of the mountains. Mountain slopes are covered with a mosaic of meadows and dwarf shrub communities. D – view of the north slope of Gilbert Ridge (elevation ca 460 m) above Lake Nicolas in Siddens Valley, Attu Island, Alaska, 21.09.2002. Soils are typically saturated

streamlet, slope of late snow area, outcrop face in *Poblia*, old pier, damp humus on cliff shelf, alpine fellfield; AT17-19 (JV), 115374 (BS), 115398 (BS), 115642 (BS), 115704 (mixed with *Diplophyllum albicans*, *Bazzania tricenata*) (BS), 115739 (BS), 115838 (BS), 115842 (BS), 115984 (BS), 116159 (BS), 116160 (BS), 116299 (BS); Alexai Point, Coast Artillery Hill, Gilbert Ridge, Jarmin Pass, Murder Point, Robinson Ridge, Terrible Mountain, USCG Loran C Station; Bering Island (Bakalin 2005); IIa.

***Bazzania tricenata* (Wahlenb.) Lindb.**

Rare; shaded bank, damp bank in gully, subalpine fleabane meadow, shaded humus hole, gully walls, mosses on streamlet bank, damp slope near cliff base; mixed with *Diplophyllum albicans*, *Marsipella emarginata*, *Herbertus* cf. *dicranus*; AT2-41, 115382, 115613, 115676, 115685A, 115690, 115840, 115855 (BS), 116005, 116043, 116197, 116208 (BS), 116232; reported by Clark & Frye (1949); Coast Artillery Hill, Gilbert Ridge, Lake Elwood, Peaceful Valley, Terrible Mountain, Thirty-Seven Hill, West Mountains; IIIb.

****Bazzania trilobata* (L.) Gray**

Uncommon; bank on mire slope, *Sphagnum compactum* mesic mire; AT25-35, 115601; Alexai Point, Peaceful Valley; VIb.

***Blasia pusilla* L.**

Rare; lava cliff; shaded humid base of cliff; 124809; reported by Clark & Frye (1948); USCG Loran A Station; Bering Island (Bakalin 2005); VII (bipolar).

***Blepharostoma trichophyllum* (L.) Dumort.**

Common; rock outcrop, shaded cliff, cliff crevices, Nootka lupine meadow, shaded bank, shaded side of hole on slope; AT19-33, AT389, 115328, 115465, 115548, 115609, 115650, 115848, 115943A, 116273, 120222, 120429; reported by Clark & Frye (1949) and Sharp & Hattori (1968); Beach Road, Coast Artillery Hill, Cape Wrangell, Casco Point, Jarmin Pass, Peaceful Valley, Robinson Ridge, Thirty-Seven Hill; Bering Island (Bakalin 2005); IVa (bipolar).

****Calycularia laxa* Lindb. & Arnell**

Uncommon; sedge wet meadow, rock outcrop, shaded cliff shelf, under boulder; AT1-27, AT88-698 (PD), AT88-707 (PD), AT88-1168 (PD), AT88-709, 115519, 124125A; this species was originally determined as *Calycularia crispula* Mitten (Davison & Smith 1992), but see Konstantinova & Mamontov (2010) who indicate it is *C. laxa* and should be updated; Jarmin Pass, Nevidiskov Creek, O'Donnell Valley,

Thirty-Seven Hill; Copper Island (Bakalin & Cherdantseva 2008); Id (Note: distribution category corrected from Ie as it occurs in both Siberia and America).

***Calypogeia azurea* Stotler & Crotz** [*C. trichomanis* auct.; not (L.) Corda]

Reported as *C. trichomanis* by Persson (1952); the identification may be based on dry material and might be doubtful; VIb.

***Calypogeia muelleriana* (Schiff.) Müll. Frib.**

Common; snowbed meadow, wet sedge meadow, ladyfern meadow, shaded humus hole, *Sphagnum compactum* tuft; AT4-44, AT41-21, AT39-38, AT42-33, AT43-26, AT43-45, AT49-49, AT61-16, 115371 (mixed with *Pellia neesiana*) (BS), 115673, 115798 (mixed with *Diplophyllum albicans*) (BS) 115822 (mixed with *Lophozia* sp.) (BS), 115910 (mixed with *Scapania uliginosa*) (BS); reported by Persson (1968); Coast Artillery Hill, Jarmin Pass, O'Donnell Valley, Peaceful Valley, Robinson Ridge, Terrible Mountain, West Massacre Valley; Bering and Copper islands (Bakalin 2005); IVa.

****Calypogeia sphagnicola* (Arnell & J. Perss.) Warnst. & Loeske**

Rare; wet sedge meadow, hard hummocks on damp slope, *Sphagnum* hummock on bank; AT42-38, 115640 (mixed with *Rhizomnium punctatum*, *Cephalozia bicuspidata*), 115280A (BS), 116051 (BS), 120303; West Massacre Valley, Jarmin Pass, Peaceful Valley, West Mountains; Bering Island (Bakalin 2005); IVa (bipolar).

****Cephalozia ambigua* C. Massal.** [*Cephalozia bicuspidata* subsp. *ambigua* (C. Massal.) R.M. Schust.]

Rare; alpine blueberry-crowberry meadow; AT33-43 (BS), 115244; Coast Artillery Hill; Bering Island (Bakalin 2005); IIa.

Species separated from *C. bicuspidata* on the basis of smaller leaf cells and different chromosome number. Recent studies based on molecular data (Vilnet et al. 2012, Feldberg et al. 2016) showed that this species nests in the robust *C. bicuspidata* clade and probably it is should be not separated on species level. But the whole *C. bicuspidata* complex (*C. bicuspidata* clade) is very complicated and needs further detailed study to clarify if the specific status of some taxa of this complex is correct.

***Cephalozia bicuspidata* (L.) Dumort.**

Common; shaded humus bank and hole, damp outcrop, wet shaded base of cliff, *Sphagnum compactum* tuft, sedge wetland, wet late snow area, damp humus bank in gully, mesic mire, Nootka lupine meadow; 115366 (mixed with *Diplophyllum albicans*, *Kurzia pauciflora*) (BS), AT25-37 (JV), AT39-40 (mixed with *Calypogeia sphagnicola*) (BS), AT42-39 (mixed with *Calypogeia muelleriana*, *Scapania* cf. *irrigua*, *Harpanthus slotovianus*), AT42-40 (BS), AT60-21 (BS), AT60-28 (BS), AT61-28, AT62-61 (mixed with *Trilophozia quinqueidentata*) (BS), 115383 (BS), 115555, mixed with *Diplophyllum albicans*, *Gymnocolea inflata*, *Nardia scalaris*, *Barbilophozia sudetica* (JV), 115799 (mixed with *Diplophyllum albicans*) (BS), 115879 (BS), 115993 (mixed with *Gymnocolea inflata*) (BS), 116161 (JV), 116170 (mixed with *Fuscocephaloziopsis albescentis*) (JV), 116262 (BS); reported by Clark & Frye (1948), Evans (1900), Macoun (1902); Alexai Point, Casco Point, Coast Artillery Hill, Lake Elwood, O'Donnell Valley, Robinson Ridge, Terrible Mountain, West Massacre Valley; Bering Island (Bakalin 2005); VII (bipolar).

***Cephaloziella divaricata* (Sm.) Schiffn.** [*Cephaloziella byssacea* Warnst.]

Rare; earth of damp area, damp cliff shelf; 115394 (BS), 115562 (JV), 115802 (BS); reported by Clark & Frye (1948); Coast Artillery Hill, Terrible Mountain; Bering Island (Bakalin 2005); IVa (bipolar).

****Cephaloziella varians* (Gottsche) Steph.**

Rare; damp area near stream, shaded damp humus of cre-

vice; 116057A (JV), 116310 (BS); Murder Point, Peaceful Valley; IIa (bipolar).

***Chiloscyphus pallescens* (Ehrh.) Dumort.**

Rare; floating in small pool of gully, narcissus anemone meadow, subalpine fleabane meadow, humus in gully; AT12-31, AT64-43, 116191 (BS), 116319 (JV); reported by Clark & Frye (1948, 1949), Persson (1952); Thirty-Seven Hill; Bering Island (Bakalin 2005); Va.

***Chiloscyphus polyanthos* (L.) Corda**

Uncommon; Nootka lupine alluvial meadow, mountain streamlet, edge of pond in wetland, bank above streamlet, alluvial meadow; 50-44 (mixed with *Conocephalum salebrosum*), AT51-42, AT345, AT346, AT2000-50-44 (BS), 115623, 115991, 116068, 116321; reported by Clark & Frye (1948); Cape Wrangell, Lake Elwood, Murder Point, Peaceful Valley, Siddens Valley, Terrible Mountain; Bering Island (Bakalin 2005); Va.

***Conocephalum salebrosum* Szwedk., Buczk. et Odrzyk.**

Abundant; ladyfern meadow, eared Indian plantain meadow, damp area near stream, shaded area by outcrop; AT13-18, AT19-20, AT65-18, AT71-21, AT102-39, AT344, 115620, 115297, 116300; reported by Clark & Frye (1948, 1949), Frye & Clark (1946); Cape Wrangell, Murder Point, Sarana Bay, Sonam Beach, West Arm Holtz Bay, West Mountains; Bering Island (Bakalin 2005); Va.

***Diplophyllum albicans* (L.) Dumort.**

Uncommon; margin of pool in crowberry mire, humus bank, shaded earth bank, damp cliff, deep shaded humus hole, base of outcrop on ridge, soil in rock crevice; AT88-1066, AT88-1067, AT88-1072, AT136, AT140, AT419, AT234 (BS), 115324A, 115364, 115389, 115606, 115707, 115889, 116129 (mixed with *Sphenolobus minutus*) (BS), 116352, 120422, 120310A; reported by Clark & Frye (1948, 1949), Frye & Clark (1946); Cape Wrangell, Casco Cove, Henderson River, Jarmin Pass, Massacre Bay, Peaceful Valley, Robinson Ridge, Temnac Cove, Terrible Mountain; Bering Island (Bakalin 2005); IIIc.

***Diplophyllum obtusifolium* (Hook.) Dumort.**

Reported by Clark & Frye (1948), Persson (1952); IVb.

***Diplophyllum taxifolium* (Wahlenb.) Dumort.**

Rare; rock outcrop, shaded cliff crevices, cliff ledge, walls of humus hole in gully; AT716, 115499A (mixed with *Diplophyllum albicans*, *Radula* sp.) (BS), 115512B, 115544B, 115552A, 116047, 116231 (mixed with *Trilophozia quinqueidentata*, *Marsipella emarginata*), 120506A; reported by Clark & Frye (1948, 1949), Persson (1952), Sharp & Hattori (1968); Casco Point, Nevidiskov Bay, Peaceful Valley, Thirty-Seven Hill; Bering Island (Bakalin 2005); IVa.

***Douinia imbricata* (M. Howe) Konstant. & Vilnet**

[*Diplophyllum imbricatum* (M.A. Howe) Müller Frib.]

Rare; open humus of cliff shelf, *Sphagnum compactum* mesic mire; AT25-33, 115952 (OL); reported by Hong (1980); Alexai Point, Beach Road; Bering Island (Bakalin 2005); IIIe.

***Douinia plicata* (Lindb.) Konstant. & Vilnet** [*Diplophyllum plicatum* Lindb.]

Rare; humus on cliff shelf, mesic mire, bog blueberry heath, steep hillside tundra, bank above streamlet gully, crowberry heath, tundra bank, side of herb-shaded gully, many-flowered sedge mire; AT21-27, AT22-30, AT24-27, AT103-29, 115586, 115691, 115952 (mixed with *Diplophyllum taxifolium*), 120170, 120310B, 120343; reported by Sharp & Hattori (1968); Beach Road, Casco Cove, Coast Artillery Hill, Gilbert Ridge, Terrible Mountain, West Mountains; Bering Island (Bakalin 2005); IIIe.

****Frullania nisquallensis* Sull.** [*F. tamarisci* subsp. *nisquallensis* (Sull.) S. Hatt., *F. tamarisci* var. *nisquallensis* (Sull.) S. Hatt.]

Rare; growing up cliff base, shaded cliff, verified genetically; 115271 (GenBank Accession No. MH325471), 115424 (GenBank Accession No. MH325472), 116193 (GenBank Accession No. MH32570); Massacre Bay, Thirty-Seven Hill; IIk.

***Fuscocephaloziopsis albescens* (Hook.) Váňa & L. Söderstr.** [*Pleurocladula albescens* (Hook.) Spruce]

Rare; rock cliff outcrop, late snowbed meadow, cliff crevice, mesic mire, seepage streamlet; AT20-33, AT22-40, AT59-27 (mixed with *Anthelia juratzkana*), AT60-13, AT414, AT477A, 116147, 116179 (mixed with *Moerckia blyttii*) (JV), 116265, 120172; reported by Davison (1993) from a collection of Sharp 9546 (TENN); Cape Wrangell, Coast Artillery Hill, Robinson Ridge, Terrible Mountain; Bering Island (Bakalin 2005); IIa.

***Fuscocephaloziopsis lunulifolia* (Dumort.) Váňa & L. Söderstr.** [*Cephalozia lunulifolia* (Dumort.) Dumort.]

Rare; shaded bank of gully, humus in maritime outcrop; mixed with *Kurzia pauciflora*, *Cephalozia bicuspidata*, *Diplophyllum taxifolium*; 115677 (BS), 116313 (BS); reported by Clark & Frye (1949), Sharp & Hattori (1968); Alexai Point, Murder Point; Bering Island (Bakalin 2005) and Copper Island (Bakalin 2010a); IVa.

***Fuscocephaloziopsis pleniceps* (Austin) Váňa & L. Söderstr.** [*Cephalozia pleniceps* (Austin) Lindb.]

Uncommon; shaded wall of gully, shaded humus of maritime outcrop, damp bank of river; 115880 (mixed with *Cephalozia bicuspidata*, *Nardia scalaris*) (BS), 116220 mixed with *Isopterygium* cf. *pulchellum* (JV), 116297 (JV), 116354 (BS & JV); reported by Persson (1952); Alexai Point, Henderson River, Murder Point, Thirty-Seven Hill; Bering Island (Bakalin 2005); IVa (bipolar).

***Gymnocolea inflata* (Huds.) Dumort.**

Abundant; bog blueberry mire, submerged in rocky stream, wet sedge seepage at streamlet head, seepage slope near outcrop, undercut pool bank in mire, black mats in streamlet, stream depression; AT42-43, AT44-31, AT88-641, AT88-646, AT88-648, AT88-658, AT88-660, AT88-1074, 115250, 115375, 115716, 115818, 115894A, 120143; reported in Davison (1993) as a collection by Sharp 9067; Abraham Bay, Coast Artillery Hill, Jim Fish Valley, O'Donnell Valley, Peaceful River Valley, Robinson Ridge, Temnac Cove, Thirty-Seven Hill, West Massacre Valley; Bering Island (Bakalin 2005); IVa.

***Gymnomitrium alpinum* (Gottsche ex Husn.) Schiffn.** [*Marsupella alpina* (Gottsche ex Husn.) Bernet]

Reported by Persson (1968); IIId.

***Gymnomitrium brevissimum* (Dumort.) Warnst.** [*Marsupella brevissima* (Dumort.) Grolle]

Rare; blowout in tundra; 116163 (JV); reported by Clark & Frye (1948) as *Gymnomitrium varians*; Robinson Ridge; Bering Island (Bakalin 2005); IIId.

***Gymnomitrium commutatum* (Limpr.) Schiffn.** [*Marsupella commutata* (Limpr.) Bernet]

Reported by Davison (1993) from a collection of Sharp 9467 (TENN); IIId.

***Gymnomitrium concinnatum* (Lightf.) Corda**

Common; boulder on slope, cliff crevice, cliff shelf, bog blueberry meadow, outcrop near summit, margin on late melt snowbed, shaded face of outcrop; AT00-33-41, AT130, 115246, 115474, 115490, 115638, 115713, 115714, 115801, 115619, 115525, 115664 (BS), 115847 (BS), 116156 (mixed with *Diplophyllum albicans*) (BS), 116205, 116349, 120158, 120482; reported by Davison (1993) from a collec-

tion of Sharp 9404 (TENN); Coast Artillery Hill, Henderson River, Peaceful Valley, Robinson Ridge, Siddens Valley, Temnac Valley, Terrible Mountain, Thirty-Seven Hill; Bering Island (Bakalin 2005); IIa (bipolar).

***Gymnomitrium corallioides* Nees**

Rare; exposed outcrop on ridge; 115813 (mixed with *Gymnomitrium pacificum*); reported by Davison (1993) from the collection S. & S. Talbot 473 (UBC); Coast Artillery Hill; Bering Island (Bakalin 2005); IIa.

***Gymnomitrium obtusum* Lindb.**

Uncommon; damp open cliff face, dry cliff, damp disturbed area; 115835 (BS), 115906 (BS), 116343 (mixed with *Diplophyllum albicans*) (BS); reported by Clark & Frye (1949); Coast Artillery Hill, Jarmin Pass, mouth of Peaceful River; IIIf (bipolar).

****Gymnomitrium pacificum* Grolle**

Rare; outcrop on alpine ridge, cliff crevices, exposed alpine gravel, rocky alpine ridge, open tundra; 115708, 115742, 115745, 115849, 115883 (BS & JV), 116146, 120178, 120392; Alexai Point, Coast Artillery Hill, Robinson Ridge, Terrible Mountain, Thirty-Seven Hill; Bering Island (Bakalin 2005); IIIe.

***Gyrothya underwoodiana* M. Howe**

Rare; shaded ditch wall in tundra; 116235; reported by Davison (1993) from the collection Sharp 9551 (TENN); Thirty-Seven Hill; VIIb (Western North America Pacific Endemic).

****Harpanthus flotovianus* (Nees) Nees**

Uncommon; wet cliff, lakeside bank, shaded wall of hole in gully, stream bank, narcissus anemone meadow, shaded wall of hole in gully, alpine spring bank, tall ladyfern meadow, Nootka lupine meadow; AT4-42, AT62-42, 116003 (mixed with *Scapania undulata*) (BS), 115750, 116093 (BS), 116236, 120292, 120348; Beach Road, Casco Bay, Lake Elwood, Peaceful Valley, Terrible Mountain, Thirty-Seven Hill; Bering Island (Bakalin 2005); IVc.

***Herbertus aduncus* (Dicks.) Gray**

Reported by Davison (1993) from a collection of Sharp 9177 (TENN); This species is more common in the area (Söderström et al. 2015), but this species was incorrectly separated from others in the past; apparently *H. aduncus* is not reported from the Commander Islands (Bakalin & Cherdantseva (2008), nor Bakalin (2010a). IIIe.

******Herbertus delavayi* Steph.**

Uncommon; floor of deep humus hole in gully, shaded all of gully; 115674 (JV), 115839 (KF), 115840 (JV); Coast Artillery Hill, Terrible Mountain; there is difficulty in placing this taxon in a geographic category as it was once considered identical with *H. sendtneri* and molecular methods may separate it; it is known from Scotland, China, Yunnan, Bhutan, British Columbia (UBC, Schofield 83644) as reported by Heinrichs et al. (2010), and now the Aleutian Islands; VIII.

Note: this species is difficult to recognize morphologically; also Juslén (2006) in her monograph of Asiatic *Herbertus* placed this species based on the type under *H. sendtneri*; based on morphological characteristics this species is in an intermediate position between *H. sendtneri* and *H. dicranus*, but not in molecular characteristics, where it is clearly different. Until now, based on specimens examined by J. Váňa and determined by molecular characteristics it is found in Schofield 115839, 115840 (in mixture with *Bazzania tricenata*).

****Herbertus dicranus* (Gottsche, Lindb. & Nees) Trevis.**

Abundant; damp bank of small gully, reddish-rusty mats on damp outcrop of mountain slope, deeply shaded gully, damp outcrop face, seepage slope, intermittent streamlet in tundra, shaded wall of hole on slope, shaded wall of gully,

steep bank of slope, shaded cliff, humus brow of sod bank, damp slope, dryish bank at upper edge of mesic mire, damp bank of mesic mire, cliff shelves, snowbed; AT1988-135, 115326, 115387, 115581, 115671, 115775, 115868, 115891, 115962, 116004, 116044, 116050, 116131, 120167, 120239, 120345, 120354, 120415; Alexai Point, Beach Road, Coast Artillery Hill, Henderson River, Jarmin Pass, Lake Elwood, Peaceful Valley, Temnac Cove, Terrible Mountain, Thirty-Seven Hill, West Mountains; unreported from the Commander Islands (Bakalin 2010a); IIIh. [AmphiPacific (disjunct Africa and India)].

****Herbertus sendtneri* (Nees) Lindb.**

Uncommon; damp bank of tundra, wall of humus hole of periodic streamlet, subalpine bank of gully, shaded wall of gully, snow bed; AT88-135, 116339 (mixed with *Myliu taylori*) (BS); 115378, 115685, 115841, 116339, 120496; Alexai Point, Coast Artillery Hill, Temnac Cove, Terrible Mountain, Thirty-Seven Hill; IIIf.

Note: until now not known from the whole of Africa and in Europe known only from Austrian Alps. Known from Aleutian Islands, Alaska and British Columbia, the mountains of Central and South America (from Mexico to Bolivia and Brazil), Gough Island, probably also Azores, in Asia from Himalayas (India and Nepal).

***Hygrobella laxifolia* (Hook.) Spruce**

Rare; bank of streamlet, wet river bank, wet cliff; 115927, 116056 (BS & JV), 116342 (mixed with *Scapania subalpina*) (BS); reported by Frye & Clark (1946); Jarmin Pass to O'Donnell Valley, Peaceful Valley; Bering Island (Bakalin 2005); IIIc.

***Jungermannia atrovirens* Dumort.**

Rare; shaded humid cliff; 115760 (JV); reported by Clark & Frye (1948); Massacre Bay; Bering Island (Bakalin 2005); IIIb.

***Jungermannia borealis* Damsh. & Vána**

Rare; seepage area, blackish masses in wet outcrop; 115344 (JV), 116260 (BS), 116337 (JV); reported by Davison (1993) from a collection of Sharp 9460 (TENN); Murder Point, Terrible Mountain; Bering Island (Bakalin 2005); IIg.

***Jungermannia exsertifolia* Steph. subsp. *cordifolia* (Dumort.) Vána**

Common; stones at bottom of herb shaded gully, shaded bottom of humus hole, seepage slope, black and green floating mat in seep, wet rock in streamlet; 120220, 115264 (JV), 115592 (JV), 115693, 115596 (JV), 116271 (JV); Coast Artillery Hill, Gilbert Ridge, Terrible Mountain, Thirty-Seven Hill, USCG Loran C Station; Bering Island (Bakalin 2005 as *Jungermannia eucordifolia* Schljakov); IIIa.

****Jungermannia pumila* With.**

Rare; wet bank of streamlet; 115683 (JV); Alexai Point; Bering Island (Bakalin 2005); IIa (bipolar).

****Kurzia makinoana* (Steph.) Grolle**

Rare; shaded humus hole in tundra; 115386 (mixed with *Nardia scalaris*) (BS); Terrible Mountain; Bering Island (Bakalin 2005); VIb.

***Kurzia pauciflora* (Dicks.) Grolle**

Rare; bank above stream, hard bank on mesic slope, peaty sod, shaded hole in slope; 115606A (BS), 115274, 115768, 115998; reported by Davison (1993) from a collection of Sharp 9475 (TENN); Peaceful Valley, Terrible Mountain, West Mountains (Kingfisher Creek); Vb.

***Lepidozia reptans* (L.) Dumort.**

Reported by Davison (1993) from a collection of Sharp 9210 (TENN); Va.

****Lophozia murmanica* Kaal.**

Rare; hard bank of mesic slope; 115999 (mixed with *Shistochloopsis incisa*, (JV); Lake Elwood; IVa.

****Lophozia guttulata* (Lindb. et Arnell) A. Evans [*Lophozia longiflora* (Nees) Schiffn. p.p.]**

Common; bank of streamlet, wet bank of tarn, shaded cliff shelf; 115629 (mixed with *Calypogeia muelleriana*, *Neoorthocaulis floerkei*) (BS), 115668 (mixed with *Buckiella undulata*, *Bazganina tricrenata*, *Neoorthocaulis floerkei*) (BS), 115808 (BS & JV); mixed with *Diplophyllum albicans*, 115853 (BS & JV), 116113 (JV), 116123, 116272 (JV); Coast Artillery Hill, Henderson Creek, Robinson Ridge, Terrible Mountain; IVa.

***Lophozia ventricosa* (Dicks.) Dumort.**

Uncommon; cliff shelf, humus in maritime outcrop; 115949 (BS), 116312 (BS); reported by Davison (1993) in Clark & Frye (1949); Beach Road, Massacre Bay, Murder Point; Bering Island (Bakalin 2005), Copper Island (Bakalin 2009 as *Lophozia longiflora*); Va.

***Lophozia wenzelii* (Nees) Steph.**

Rare; old timber from derelict building; 116103 (mixed with *Ptilidium pulcherrimum*) (BS); reported by Davison (1993) from a collection of Sharp 9368 (TENN); Peaceful Valley; Bering Island (Bakalin 2005); IVa.

***Lophozopsis excisa* (Dicks.) Konstant & Villnet [*Lophozia excisa* (Dicks.) Dumort.]**

Reported by Clark & Frye (1948), Persson (1952); Bering Island (Bakalin 2005); IVa (bipolar).

***Marchantia polymorpha* L.**

Rare; Lynbye sedge poor fen; AT15-31; reported by Clark & Frye (1948), Frye & Clark (1946); Peaceful Valley; Bering Island (Bakalin 2005); VII (bipolar).

****Marsupella apiculata* Schiffn. [*Gymnomitrium apiculatum* (Schiffn.) Müll.Frib.]**

Rare; exposed alpine ridge; 115740 (mixed with *Gymnomitrium concinnatum* (JV); Robinson Ridge; Bering Island (Bakalin 2005); IIa.

****Marsupella aquatica* (Lindenb.) Schiffn. [*M. emarginata* var. *aquatica* (Lindenb.) Dumort.]**

Rare; cliff crevices; 115846 (BS); Coast Artillery Hill; IIIa.

***Marsupella emarginata* (Ehrh.) Dumort.**

Abundant; seepage in slope, seep in rock crevice, damp cliff shelf, damp cliff, undercut of pool bank in mire, old road bed, shaded cliff crevices, streamlet in slope, wet outcrop, black masses in late snow patch, wet alpine tundra slope, ditch near road, rock cliff outcrop; AT88-603, AT88-604, AT88-650, AT88-718a, 413b, 115824A (BS), 115827 (OL), 115828 (BS), 115856 (BS), 115861 (BS) 115924 (BS), 115942 (mixed with *Scapania curta*) (BS), 115943 (BS), 120096 (BS), 116114 (BS), 116152 (BS), 116166 (JV), 116174 (BS), 116182 (BS); reported by Clark & Frye (1949); Alexai Point, Beach Road, Cape Wrangell, Chirikof Point, Coast Artillery Hill, Henderson Creek, Jarmin Pass, Jim Fish Valley, Peaceful Valley, Robinson Ridge, West Arm Nevidiskov Bay; Bering Island (Bakalin 2005); IIIa (bipolar).

***Marsupella sparsifolia* (Lindb.) Dumort.**

Rare; wet seepage depression; 120164; Coast Artillery Hill; Copper Island (Bakalin & Cherdantseva 2008); II d (bipolar).

***Marsupella sphacelata* (Giessecke ex Lindenb.) Dumort.**

Uncommon; late snow melt slope, submerged in pool, cliffs by streamlet, *Sphagnum* mire, wet slope, old runway pavement, snow-melt slope; AT61-32 (BS), AT88-808 (PD), 115256, 115726 (BS & JV), 115805 (mixed with *Barbilophozia sudetica*, *Scapania paludosa*) (BS), 115887A (BS); re-

ported by Davison (1993) from a collection of Sharp 9531 (TENN); Alexai Point, Coast Artillery Hill, Jarmin Pass, Peaceful River, Robinson Ridge, O'Donnell Valley, Thirty-Seven Hill; IIIf.

***Marsupella stableri* Spruce** [*Marsupella boeckii* var. *stableri* R.M. Schuster]

Rare; damp alpine outcrop, streamlet margin, late snowmelt slope, 116165 (OL), 116175 (BS), 120398 (OL), 120464 (OL); reported by Davison (1993) from a collection of Sharp 9505 (TENN); Robinson Ridge, Siddens Valley; Bering Island (Bakalin 2005); IIIf.

***Metacalypogeia cordifolia* (Steph.) Inoue** [*Calypogeia cordifolia* Steph.]

Rare; damp shaded cliff near stream; 116306 (mixed with *Blepharostoma trichophyllum*, *Fuscocephaloziopsis* cf. *lunulifolia*) (BS); reported by Davison (1993) from a collection of Sharp 9052 (TENN); Murder Point; VIb.

***Metzgeria conjugata* Lindb.**

Uncommon; rock outcrop, shaded cliff, damp bank in gully, shaded humid cliff shelves; AT88-708, 115425, 115870, 115896, 116207, 120456; reported by Davison (1993) from the collection S. & S. Talbot 689 (UBC); Alexai Point, Gilbert Ridge, Jarmin Pass, Thirty-Seven Hill, West Arm Nevisdiskov Bay; Va. Söderström et al. (2010) stated that *Metzgeria conjugata* is a complex taxon; accordingly, we are conservative in naming the Attu specimens.

***Metzgeria pubescens* (Schränk) Raddi** [*Apometzgeria pubescens* (Schränk) Kuwahara]

Rare; deeply shaded wall of gully; 120355; reported by Frye & Clark (1946); West Mountains; IIIf (bipolar).

***Moerckia blyttii* (Mørch) Brockm.**

Uncommon; peaty bank of alpine streamlet, *Sphagnum* in bog blueberry mire, Pyrenean sedge snowbed meadow, mountain maretail snowbed meadow, peaty bank of pond, bank of streamlet in alpine saddle; AT59-23, AT88-655, 115654, 116179 mixed with *Fuscocephaloziopsis albescens* (JV), 120155, 120262; reported by Davison (1993) from collection of Sharp 9214; Coast Artillery Hill, Jim Fish Valley, Robinson Ridge, Thirty-Seven Hill; Bering Island (Bakalin 2005); IIId.

***Moerckia hibernica* (Hook.) Gottsche**

Rare; rock cliff outcrop, AT457; reported by Davison (1993) from the collection S. & S. Talbot 457 (UBC); Cape Wrangell; Vb.

***Mylia taylorii* (Hook.) Gray**

Common; mire bank, damp bank in tundra, seepy bank of tundra, *Sphagnum* on tundra slope, caltha-leaf avens meadow, mire bank, seepage slope near outcrop, damp slope near ridge top, ditch by runway, shaded humus hole on slope, *Sphagnum compactum* mesic mire, Pyrenean sedge snowbed meadow, wall of gully, side of herb-shaded gully, damp bank in tundra, ditch by airport runway; AT2-49, AT25-40, AT60-36, 115314, 115380, 115605 (mixed with *Sphenobolus saxicola*, *Herbertus* cf. *dicranus*, *Diplophyllum albicans*) (BS), 115611, 115657, 115817, 115826, 115388, 115602, 116339 (mixed with *Herbertus sendtneri*) (BS), 120299, 120307; reported by Davison (1993) from collection of Llano 1383e (UBC); Alexai Point, Coast Artillery Hill, Murder Point, Peaceful Valley, Terrible Mountain, West Mountains; IIIb.

****Nardia breidleri* (Limp.) Lindb.**

Rare; Alaska arnica – Nootka lupine fellfield; AT26-29; Robinson Ridge; Bering Island (Bakalin 2005); IIId.

****Nardia geoscyphus* (De Not.) Lindb.**

Rare; shaded side of hole in slope, peat moss tuft in mesic

mire; 115649 (BS & JV), 115658; Robinson Ridge; Bering Island (Bakalin 2005); IIa.

****Nardia japonica* Steph.**

Rare; damp outcrop; 115919 (BS); Jarmin Pass; Bering Island (Bakalin 2005); IIh.

***Nardia scalaris* Gray**

Abundant; damp slope at head of streamlet, open damp area in ridge, earth bank, earth base of huge boulder, wet cliff, rock outcrop, undercut pool bank in alpine blueberry mire, mineral soil in rock crevice, damp edge of stream, shaded earth bank, humus clods on barren ridge, wet bank above stream, shaded cliff shelves, sand dune, snowbed, fellfield, crowberry mire, earth base of huge boulder; AT123, AT221, AT18-39, AT28-36, AT88-651, AT88-653, AT88-1069, AT104-34, 115241, 115340, 115287A, 115359, 115732 (mixed with *Nardia geoscyphus*, *Barbilophozia sudetica*) (BS & JV), 115804 (BS), 115809 (mixed with *Barbilophozia sudetica*) (BS), 116058 (BS), 116138, 116198 (BS), 116357 (mixed with *Diplophyllum albicans*) (BS); reported by Clark & Frye (1948), Frye & Clark (1946); Beach Road, Casco Cove, Coast Artillery Hill, Henderson River, Jarmin Pass, Jim Fish Valley, Peaceful Valley, Robinson Ridge, Temnac Cove, Terrible Mountain, Thirty-Seven Hill, West Mountains; Bering Island (Bakalin 2005); IIIc.

***Neoorthocaulis floerkei* (F. Weber & D. Mohr) L. Söderstr., De Roo & Hedd.** [*Barbilophozia floerkei* (Weber & Mohr) Loeske]

Common; wet edge of pond, bank of mire slope, alpine slope, wet late snowbed area, alpine blueberry heath, building foundation; mixed with *Barbilophozia sudetica*, crowberry tundra, dry outcrop shelf; AT16-29, 115248 (mixed with *Solenostoma* sp.) (BS), 115390 (BS), 115600 (BS), 115613A (BS), 115630 (BS), 115729, 115733 (BS), 115886A (BS), 115908, 116150, 116184 (mixed with *Barbilophozia sudetica*) (BS), 116254 (BS), 116258 (BS), 120154, 120342, 120359, 120372; reported by Clark & Frye (1948); Jarmin Pass, Peaceful Valley, Robinson Ridge, Terrible Mountain, USCG Loran C Station; Bering Island (Bakalin 2005) as *Orthocaulis floerkei*; IIIb.

***Pellia endiviifolia* (Dicks.) Dumort.**

Rare; shaded bank; 115538; reported by Clark & Frye (1948), Frye & Clark (1946); Thirty-Seven Hill; Vb.

***Pellia neesiana* (Gottsche) Limpr.**

Uncommon; bottom of humus hole, shaded cliff shelves, shaded bank; 115367, 116137, 116148, 120201; reported by Clark & Frye (1948), Frye & Clark (1946); Henderson River, Lake Elwood, Robinson Ridge, Terrible Mountain; Bering Island (Bakalin 2005); IVa.

***Plagiochila asplenioides* (L.) Dumort.**

Reported by Davison (1993) as *Plagiochila arctica* from Clark & Frye (1949), Persson (1968); Ic.

****Plagiochila porelloides* (Torr. ex Nees) Lindenb.** [*P. asplenioides* ssp. *porelloides* (Torr. ex Nees) Kaal.]

Rare; up base of cliff in outcrop on slope, humus bank of lake shore, deeply shaded crevices of seaside outcrop; 115272, 120484, 120532; Casco Cove, Siddens Valley, West Mountains; Bering Island (Bakalin 2005); Va.

***Plagiochila schofieldiana* Inoue**

Uncommon; overhanging sod in seep streamlet, wall of hole in gully, shaded cliff ledge, walls of damp hole in gully, bank of herb shaded gully; 115321, 115513, 115694, 115903, 116045A, 116187, 116238 (mixed with *Blepharostoma trichophyllum*, *Diplophyllum taxifolium*, *Diplophyllum albicans*, *Scapania* sp., *Acrobolbus ciliatus*), 120214, 120358; reported by

Schuster (1980); Gilbert Ridge, Jarmin Pass, Peaceful Valley, Thirty-Seven Hill, West Mountains; VIb. [Endemic to Pacific Northwest North America].

***Porella cordaeana* (Huebener) Moore**

Uncommon; shaded herb gully, shaded cliff shelf; 115789, 120423; reported by Persson (1952); Beach Road, Terrible Mountain; IIIg.

***Porella fauriei* (Steph.) S. Hatt.** [*P. vernicosa* Lindb. subsp. *fauriei* (Steph.) M. Hara]

Uncommon; dune turf on cliff shelf, floor of steep herb slope, cliff shelf base; AT23-36, 115419, 115700, 120448; reported by Hattori (1970); Alexai Point, Gilbert Ridge; VIc.

****Preissia quadrata* (Scop.) Nees.**

Rare; shaded cliff; 115867; Alexai Point; Bering Island (Bakalin 2005); IVa.

***Ptilidium ciliare* (L.) Hampe**

Uncommon; crowberry heath, herb slope, old timber from derelict building; AT6-19, 115612, 116250, 120341; reported by Frye & Clark (1946); Terrible Mountain, Peaceful Valley, Henderson River, West Mountains; Bering Island (Bakalin 2005); IVa (bipolar).

****Ptilidium pulcherrimum* (Weber) Vain.**

Rare; old timber from derelict building; 116104 (mixed with *Lophozia wenzelii*); Peaceful Valley; Va.

***Radula complanata* (L.) Dumort.**

Uncommon; rock outcrop; AT88-694, AT694, AT704 (BS), 115466, 115774, 116229, 120444, 120449; reported by Clark & Frye (1948), Frye & Clark (1946); Alexai Point, Gilbert Ridge, Nevidiskov Creek, Terrible Mountain; Bering Island (Bakalin 2005, 2010a); Va.

***Radula obtusiloba* Steph.** [R. *obtusiloba* subsp. *polyclada* (A. Evans) S. Hatt., R. *polyclada* A. Evans]

Rare; shaded cliff shelf, rock outcrop, damp cliff crevices; 410, 469, 115508, 115539, 115550, 115957 (BS), 115961, 116209, 116278, 120241, 120352, 120494; reported by Clark & Frye (1948), Frye & Clark (1946), Persson (1947); Beach Road, Cape Wrangell, Casco Point, Gilbert Ridge, Thirty-Seven Hill, Nevidiskov Creek, Terrible Mountain, West Mountains; Ve.

****Radula prolifera* Arnell**

Uncommon; damp overhang along streamlet seepage, damp shaded base of cliff, walls of herb gully, deeply shaded gully; 115329, 115938, 115703, 115792, 120346; Beach Road, Gilbert Ridge, Kingfisher Creek, Terrible Mountain, West Mountains; Copper Island (Bakalin 2010a). Id.

***Riccardia chamedryfolia* (With.) Grolle**

Rare; damp bank of streamlet; 116267; reported by Davison (1993) from a collection of Sharp 9081 (TENN); Terrible Mountain; Va.

***Riccardia multifida* (L.) Gray**

Rare; shaded damp bank by waterfall, damp bank of streamlet; 115368 (BS), 116266; reported by Clark & Frye (1948), Persson (1952); Terrible Mountain; Va (bipolar).

***Scapania curta* (Mart.) Dumort.**

Rare; shaded bank of river; 116359 (BS); reported by Clark & Frye (1948); Henderson River; Bering Island (Bakalin 2005); IVa.

****Scapania degenii* Schifff. ex Müll. Frib.** [*Scapania brevicaulis* Taylor]

Rare; cliff shelf; 115421 (BS & JV); USGS Loran C Station; IIa.

***Scapania irrigua* (Nees) Nees**

Rare; Lyngbye sedge wet meadow, AT41-20 (mixed with *Gymnocolea inflata*) (BS & JV), AT42-28 (JV; mixed with *Cephalozia bicuspidata*), AT43-29 (mixed with *Cephalozia bicuspidata*, *Trilophozia quinquedentata*) (BS); reported by Clark & Frye (1948); O'Donnell Valley, West Massacre Valley; Bering Island (Bakalin 2005); IVa

***Scapania paludosa* (Müll. Frib.) Müll. Frib.**

Abundant; seepage slope, among sedges at pond margin, seepage, shaded wet hole in gully, wet cliff, damp area, shaded wet floor of humus hole in gully, edge of old runway, seepage slope, wet late snowbed area; 88-606 (PD), AT60-13 (BS), AT61-27, 115298A (BS), 115400A (BS), 115593A (BS), 115695 (mixed with *Dichodontium pellucidum*) (BS), 115749 (BS), 116010 (BS), 116032 (mixed with *Diplophyllum albicans*, *Blepharostoma trichophyllum*) (BS), 116046 (BS), 116089 (BS), 116149 (BS); reported by Persson (1968); Alexai Point, Beach Road, Chirikof Point, Coast Artillery Hill, Kingfisher Creek, Lake Elwood, Peaceful Valley, Robinson Ridge, USCG Loran C Station; Bering Island (Bakalin 2005); IIb.

****Scapania parvifolia* Warnst.** [*S. scandica* (Arnell & H. Buch) Macvicar form *parvifolia* (Warnst.) Schljakov]

Rare; cliff ledge; 115552 (BS); Casco Point; Bering Island (Bakalin 2005); VIII.

***Scapania scandica* (Arnell & H. Buch) Macvicar**

Uncommon; cliff shelf, damp area by road, wet sedge meadow; AT39-36 (BS), AT39-37 (mixed with *Cephalozia bicuspidata*), 115933 (BS), 115552 (BS), 115982 (BS); reported by Davison (1993) from a collection of Sharp 9136 (TENN); Beach Road, O'Donnell Valley, USCG Loran C Station; IIb.

***Scapania subalpina* (Nees ex Lindenb.) Dumort.**

Rare; peaty stream bank, roadside ditch bank, alluvial valley, wet cliff; AT88-800, 115591 (mixed with *Calypogeia muelleriana*) (BS), 115754 (OL), 115885 (mixed with *Hygrobiella laxifolia*) (BS), 116077 (JV); reported by Davison (1993) from a collection of Sharp 9323 (TENN); Coast Artillery Hill, O'Donnell Valley; Bering Island (Bakalin 2005); IVa.

***Scapania uliginosa* (Lindenb.) Dumort.**

Uncommon; water of streamlet, seep area near streamlet, shaded wet depression, damp area, floating in spring pool margin, Lyngbye sedge wet meadow, wet depression in mesic mire, wet depression of seepy slope, wetland margin, seepage area of tufted bulrush slope; AT41-24, AT42-27, AT43-25, 115320, 115333, 115397, 115595A, 115635, 115662, 115794, 115652 (mixed with *Marsupella emarginata*), 115653 (mixed with *Marsupella emarginata*) (BS), 115834 (BS), 116016 (BS), 116049 (mixed with *Scapania paludosa*) (BS), 116214 (BS), 120252, 120256, 120288, 120297, 120516, 120168; reported by Macoun (1902); Coast Artillery Hill, Jarmin Pass, Kingfisher Creek, Lake Elwood, Peaceful Valley, Terrible Mountain, Thirty-Seven Hill, USCG Loran C Station; IIb.

***Scapania undulata* (L.) Dumort.**

Abundant; damp slope, seepage near road, deep humus hole in tundra, rocks in subalpine streamlet, black masses in wet area, seep in rock by waterfall, boulder in stream, Lyngbye sedge wet meadow, boulder in stream; AT601, 115266 (BS), 115338A (mixed with *Jungermannia borealis*, *Blindia acuta*) (BS), 115389A (BS), 115686 (BS), 115806 (mixed with *Marsupella emarginata*) (BS), 115869 (BS), 116052 (mixed with *Calliargon* sp.) (BS), 116322 (BS); reported by Clark & Frye (1948, 1949), Frye & Clark (1946); Alexai Point, Chirikof Point, Coast Artillery Hill, Murder Point, Peaceful Valley, Terrible Mountain, USCG Loran C Station, West Massacre Valley; Bering Island (Bakalin 2005); IIIa.

****Schistochilopsis grandiretis* (Lindb. ex Kaal.) Konstant.** [*Lophozia grandiretis* (Lindb. in Kaal.) Schiffn.]

Rare; wet bank above stream, damp bank of streamlet; 115361 (BS & JV), 116268 (mixed with *Scapania uliginosa*, *Riccardia multifida*, *Calypogeia* cf. *sphagnicola*) (JV); Terrible Mountain; IIa.

***Schistochilopsis incisa* (Schrad.) Konstat.** [*Lophozia incisa* (Schrad.) Dumort.]

Uncommon; late snow bed area, sheltered area at base of outcrop, shaded outcrop, damp cliff on humus; 115735 (BS), 115736 (mixed with *Barbilophozia sudetica*) (BS), 116143; reported by Davison (1993); Henderson River, Kingfisher Creek, Robinson Ridge; Bering Island (Bakalin 2005); IVa.

***Schistochilopsis opacifolia* (Culm. ex Meyl.) Konstant.** [*Lophozia opacifolia* Culm. ex Meyl., *L. incisa* subsp. *opacifolia* (Culm. ex Meyl.) R.M. Schust. et Damsh.]

Rare; wet late snow area; 116143; reported by Davison (1993) as *L. incisa* subsp. *opacifolia*; Robinson Ridge; Bering Island (Bakalin 2005); IIa.

****Schljakovianthus quadrilobus* (Lindb.) Konstant. et Vilnet** [*Barbilophozia quadriloba* (Lindb.) Loeske, *Lophozia quadriloba* (Lindb.) A. Evans]

Rare; flatlands near house foundation; 116090 (BS); Pleasant Valley. IIb.

***Solenostoma fusiforme* (Steph.) R.M. Schust.** [*Jungermannia fusiformis* (Steph.) Steph.]

Rare; wet outcrop; reported by Vána (1975); IIh.

***Solenostoma obovatum* (Nees) C. Massal.** [*Jungermannia obovata* Nees]

Rare; seep in rock crevice by waterfall, damp bank by stream, rock outcrop; AT604 (BS & JV, mixed with *Marsupella emarginata*), AT691 (mixed with *Cephalozia bicuspidata*), 116060, 116065 (JV), 116069 (JV), 116070 (JV), 116118 (BS), 116280 (BS & JV, mixed with *Cephalozia bicuspidata*, *Marsupella emarginata*); reported by Clark & Frye (1948, 1949), Frye & Clark (1946); Chirikof Point, Henderson River, Peaceful Valley, Terrible Mountain, West Arm Nevidiskov Bay; Bering Island (Bakalin 2005 as *Plectocolea obovata*); IIa.

****Solenostoma rubrum* (Gottsche) R.M. Schust.** [*Jungermannia rubra* Gottsche, *Nardia rubra* (Gottsche) A. Evans]

Rare; 115589 (JV), 116350 (JV); peaty stream bank, damp bank of river; Coast Artillery Hill, Henderson River; IIIe.

***Solenostoma sphaerocarpum* (Hook.) Steph.** [*Jungermannia sphaerocarpa* Hook.]

Reported by Clark & Frye (1948); IVa (bipolar).

***Sphenolobus minutus* (Schreb. ex D. Crantz) Berggr.** [*Anastrophyllum minutum* (Schreb.) R.M. Schuster]

Common; damp outcrop, alpine blueberry heath, bank of humus hole in gully, cliff crevice, pendant humus over outcrop, crowberry heath, humus on cliff shelf, on mound at edge of seepage slope, bluejoint-alpine blueberry heath; AT36-42, AT 37-43, 115546 (BS), 115692, 115854, 116344, 120442; reported by Persson (1952); Alexai Point, Casco Point, Coast Artillery Hill, Gilbert Ridge, Henderson River, Terrible Mountain; Bering Island (Bakalin 2005); IVa (bipolar).

***Sphenolobus saxicola* (Schrad.) Steph.** [*Anastrophyllum saxicola* (Schrad.) R.M. Schuster]

Common; crowberry and alpine blueberry heaths, tufted clubbrush mesic mire; AT 6-42, AT 36-41, AT37-36, AT 22-41; reported by Persson (1952); Gilbert Ridge, Terrible Mountain; IVa.

***Trilophozia quinqueidentata* (Huds.) Bakalin** [*Tritomaria quinqueidentata* (Huds.) H. Buch]

Common; alpine blueberry heath, shaded bank, sedge wetland, ditch near road, wall of humus hole, streamlet bank, side of herb shaded gully, fellfield; 115615 (BS), 116001 (BS), 116241 (mixed with *Racomitrium lanuginosum*), 116256 (mixed with *Fuscocephaloziaopsis pleniceps*) (BS); reported by Clark & Frye (1948); Coast Artillery Hill, Peaceful Valley, Lake Elwood, Terrible Mountain, West Arm Nevidiskov Bay; Bering Island (Bakalin 2005); IVa.

Analysis of the flora

The distribution patterns (Konstantinova 2000) of 112 Attu liverworts species indicate three geographic elements dominate the flora: 1) arctomontane (30 species, or 26.1 %), 2) arctoboreomontane (27 species, or 23.4 %), and 3) montane (23 species, 20 %). These are followed by a boreal element which includes a moderate number of species (16 species, or 13.9 %), a smaller temperate component (7 species or 6.1 %), and a nearly absent arctic element (2 species, or 1 %) (Table 1). In the arctomontane, arctoboreomontane, and boreal elements, many of the species are circumpolar, or nearly circumpolar, and account for approximately 78 % of the flora.

Comparison of the major geographical elements for the North Holarctic (Konstantinova 2000) with those of Attu Island is given in Table 2. With the exception of the higher percent of the Arctic species in the North Holarctic region (16 %), geographic patterns exhibited for Attu Island are similar. This is consistent with the interpretation of Tuhkanen (1984), that Attu Island is boreal and not Arctic. In the central Aleutian Islands, Talbot et al. (2010) reported a higher percentage of boreal plants, 25 %, than arctic-alpine, 12 %, and a mixture of arctic and boreal classes, 6 %. Additionally, Bakalin (2010b) indicated that the Kuril Island Archipelago extends 1200 km in a northeast direction from Hokkaido Island, Japan, uniting the boreal flora of southern Kamchatka with the temperate flora enriched with subtropical elements of Hokkaido.

Commonness of species

Table 3 indicates the most important liverwort species within the landscape in terms of commonness. Abundant species included *Anthelia julacea*, *A. juratzkana*, *Conocephalum salebrosum*, *Gymnocolea inflata*, *Herbertus dicranus*, *Marsupella emarginata*, *Nardia scalaris*, *Scapania paludosa*, while common species were *Barbilophozia sudetica*, *Blepharostoma trichophyllum*, *Calopogeia muelleriana*, *Cephalozia bicuspidata*, *Jungermannia excertifolia* subsp. *cordifolia*, *Lophozia longiflora*, *Mylia talorii*, *Neorthiscaulis floerkei* and *Sphenolobus minutus*.

Comparison with the Commander Islands

A total of 112 liverwort species are reported from the Commander Islands (Bakalin 2010a). Of these species, 43 liverworts, or 38 %, have not been reported from Attu Island (Table 4): *Athalamia hyalina*, *Barbilophozia hatcheri*, *Calypogeia integristipula*, *Cephalozia elachista*, *C. uncinata*, *Conocephalum japonicum*, *Eremonotus myriocarpus*, *Fuscocephaloziaopsis leucantha*, *F. pachycaulis*, *Jungermannia excertifolia* subsp. *excertifolia*, *J. polaris*, *Lophocolea heterophylla*, *L. minor*, *Lophozia savicziae*, *L. schusterana*, *L. silvicola*, *L. silvicoloides*, *Lophoziaopsis pellucida*, *Marsupella sprucei*, *Mesoptychia gillmanii*, *M. heterocolpos*, *Mylia*

Table 1. Percent distribution of Attu Island, Alaska, liverwort species in phytogeographic categories following the North Holarctic categories of Konstantinova (2000).

Phytogeographic category	Number of species	Percent of flora
I. ARCTIC		
d. Siberian-American	2	1.8
II. ARCTOMONTANE		
a. Circumpolar	16	14.3
b. Subcircumpolar	3	2.6
c. Disjunctive	6	5.4
e. Euro-Siberian	1	0.9
h. Eurasian-West American	3	2.6
k. Siberian-West American	1	0.8
III. MONTANE		
a. Circumpolar	4	3.6
b. Subcircumpolar	8	7.1
c. Amphioceanic	3	2.6
e. Pacific	4	3.6
f. Disjunctive	2	1.8
g. Euro-West American	1	0.9
IV. ARCTOBOREOMONTANE		
a. Circumpolar	25	22.3
b. Subcircumpolar	1	0.9
c. Amphioceanic	1	0.9
V. BOREAL		
a. Circumpolar	12	10.7
b. Subcircumpolar	3	2.6
c. Euro-American	1	0.9
VI. TEMPERATE		
b. Amphioceanic	6	5.3
c. Pacific	1	0.9
VII. COSMOPOLITAN	4	3.6
VIII. UNCLEAR	4	3.6
TOTAL	112	100

anomala, *Nardia compressa*, *Neoorthocaulis binsteadii*, *Obtusifolium obtusum*, *Odontoschisma elongatum*, *Plagiobchila arctica*, *Porella platyphylla*, *Ptilidium californicum*, *Riccardia aeruginosa*, *R. latifrons*, *Saccobasis polita*, *Sauntera alpina*, *Scapania cuspiduligera*, *S. hyperborea*, *S. kaurinii*, *S. ligulata*, *S. mucronata*, *S. obscura*, *Schizakovia kumzeana*, *Solenostoma gracillimum*, *S. hyalinum*, *S. infusum* and *S. obovatum* (Bakalin 2010a). The number of Attu liverworts present in the Commander Islands was 71, or 63 %.

A total of 112 liverwort species were reported from Attu Island, of these 48 liverwort species, or 41 % have not been reported from the Commander Islands (Table 4): *Acrobolbus ciliatus*, *Anastrepta orcadensis*, *Barbilophozia barbata*, *Bazzania tricenata*, *B. trilobata*, *Calypogeia azurea*, *Diplophyllum obtusifolium*, *Frullania nisqualensis*, *Gymnomitrium commutatum*, *G. obtusum*, *Gyrothyra underwoodiana*, *Herbertus delavayi*, *H. dicranus*, *H. sendtneri*, *Kurzia pauciflora*, *Lepidozia reptans*, *Lophozia murmanica*, *L. guttulata*, *Marsupella aquatica*, *M. sphacelata*, *Metacalypogeia cordifolia*, *Metzgeria conjugata*, *M. pubescens*, *Moerckia hibernica*, *Mylia talorii*, *Pellia endiviifolia*, *Plagiobchila asplenoides*, *P. schofieldiana*, *Porella cordaeana*, *P. fauriei*, *Ptilidium pulcherrimum*, *Radula obtusiloba*, *Riccardia chamedryfolia*, *R. multifida*, *Scapania degenii*, *S. uliginosa*, *Schistochilopsis grandirentis*, *S. opacifolia*, *Solenostoma fusiforme*, and *S. rubrum*. These data indicated the liverworts of the region were generally widespread species, but there are large gaps in species distributions between the eastern and western portions of the region.

Table 2. Percent distribution of liverwort species in major North Holarctic elements (Konstantinova 2000) compared to Attu Island, Alaska (present study).

Geographic element	North Holarctic	Attu Island
Arctic	16	2
Arctomontane	24	27
Montane	16	20
Arctoboreomontane	19	24
Boreal	15	14
Temperate	10	6
Cosmopolitan	1	4
Total	100	100

Table 3. Frequency of occurrence of liverwort species in four commonness classes within Attu Island, Alaska.

Commonness category	Number of species	Percent of flora
Rare	54	48.2
Uncommon	24	21.4
Common	11	9.8
Abundant	9	8.1
No data*	14	12.5
Total	112	100

* Published without commonness data.

Liverworts excluded from Attu Island list

Two unconfirmed *Lejeunea* species were reported by Davison (1993:224) in a collection of A.J. Sharp 9039 and 9039c (TENN) but no firm determination was made: *Lejeunea* cf. *flava* and *L.* cf. *stevensiana* growing in admixture with *Acrobolbus ciliatus*. We searched for these two species at what appeared to be the same and similar sites but did not locate them. Their presence is therefore in doubt, and they may have been incorrectly named. From a geographical perspective, *L. flava* is a Pantropical species with incursions into the temperate zone, and *L. stevensiana* is a Himalayan species not occurring outside the Himalayas. We excluded both species from the flora until a definite determination may be made.

DISCUSSION

This research represented an essential contribution to the understanding of liverwort distribution in a strategic location that bridges the flora between Asia and North America. Our list of Attu liverworts was based on modern liverwort taxonomy which was established through a collaboration of taxonomic specialists (Söderström et al. 2015, 2016). The listed species often reference earlier names from the literature as an aid for the reader.

Our list of liverworts collected from Attu Island updates assessments of liverwort diversity on Attu Island – these results confirm the presence of many previously reported species, add new site records, and add a number of new species records for Attu Island. These include the addition of 34 species to the liverwort flora of Attu Island and markedly increases the total number of species from ca 84 reported by Davison (1993) to a total of 112 species. This 30 % increase suggested previous knowledge of Attu liverwort diversity was incomplete and the liverwort flora is richer than previously known. For logistical reasons, our

Table 4. Comparison of the numbers of liverwort species present on Attu Island, Alaska, and the Commander Islands, Russian Federation (with percentages based on the total liverwort flora).

Region	Attu Island	Commander Islands
Total number of species	112	112
Number of Attu species	present on Commander Islands – 66 (59%)	absent on Commander Islands – 48 (41%)
Number of Commander species	absent on Attu Island – 41 (37%)	present on Attu Island – 68 (59%)

study concentrated primarily on the easternmost portions of Attu Island; future field studies from a wider area are anticipated to yield new records. One species, *Herbertus delavayi* was new to the Aleutian Islands and Alaska; its nearest known reported record is from Haida Gwaii, previously known as the Queen Charlotte Islands, British Columbia (Heinrichs et al. 2010).

The Commander Islands and Attu Island are geographically separated by 300 km. For the vascular flora, Tatewaki (1963:194) pointed out a distinct difference between the Commander Islands and the U.S. Aleutian Islands and proposed the existence of a ‘floristic depression’ between the two districts. Our results, combined with the work of Bakalin & Cherdantseva (2008), support the concept of floristic depression in liverwort distribution observed in vascular plants. The significance of *Hultenia* as a link between the liverwort floras of Asia and America, and the Tatewaki-line in dividing the Aleutian Islands from the Commander Islands is of great value in liverwort bryogeography (Bakalin & Cherdantseva 2008). For example, *Hultenia* may have served as a bridge between North America and Asia harboring relicts of Cold and Warm Pleistocene epochs (Bakalin & Cherdantseva 2008).

Our study provided newly reported species and further distributional evidence. For a number of species, the Aleutians are outposts of their western or eastern extremities of distribution. However, while *Hultenia* may play a significant role as a migration path for liverworts (Bakalin & Cherdantseva 2008), it is not possible to indicate the exact number of species – some Aleutian arc taxa may be isolated and separated from their main distribution as relicts of warmer epochs. Regardless, our list of Attu Island liverwort species provided a baseline to interpret future floristic change from factors such as climate and ash deposition from volcanic eruption on the liverwort flora.

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