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.

Key words: Hepaticae, phytogeography, northern boreal, hyperoceanic, Bering Land Bridge

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 Atu Island, the westernmost island in the United States, toward the Commander Islands of Russia, which comprise the westernmost part 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 phytogeographic pattern of Attu liverworts with liverwort distribution in circumpolar regions to provide a comparative context, including comparing the liverwort flora of Attu island 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 (Soderstrom 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 Wiscon-
sian 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 (Tsvektov 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, Patrik & 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 oceanicity, Attu is relatively more hyperoceanic (O3) than Bering (O2; 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 Wilfred 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. Alexei 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°55’N, 173°23’E; 11 m;
20. Siddens Valley, 52°52’N, 173°14’E; 30–10 m;
21. Sonam Beach, 52°48’N, 173°06’E; 15 m;
22. Temnae 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-line 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).


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 indicates 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 delanyi*, 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.

**Acroblus ciliatus** (Mitt.) Schifflin.

Rare; shaded wall, humus hole in gully, 116047A (mixed with *Diplophyllum taxifolium*) (BS); reported by Sharp & Hart (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; Ilc.

**Anastrepta orcadensis** (Hook.) Schifflin.

Rare; side of humus hole on slope, sedge wetland, 115667 (mixed with *Diplophyllum albicans*) (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, 115237, 115491A, 115577, 115816, 115854, 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); IIa.

**Anthelia juratzkana** (Limpr.) Trevis.

Abundant; dryish tundra crust; 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.

**Barbiloaphozia barbata** (Schmidel ex Schreb.) Loeske [*Laphozia bartata* (Schmidel) Dumort.]

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

**Barbiloaphozia lycopodiioides** (Wallr.) Loeske [*Laphozia lycopodiioides* (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.

**Barbiloaphozia sudetica** (Nees ex Huebner) L. Söderstr., De Roo et Hedd. [*Laphozia sudetica* (Nees ex Huebner) Grolle]

Common; dark strands overgrowing Sphagnum in tundra, Sphagnum at edge of pond base of terrace bank, bank of...
Liverworts from Attu Island, Alaska with comparison to the Commander Islands, Russia

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 Pohlia, old pier, damp humus on cliff shelf, alpine fellfield; AT17-19 (JV), 115374 (BS), 115398 (BS), 115642 (BS), 115704 (mixed with Diplophyllum albicans, Bazzania tricornata) (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 tricornata (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, Marsupella emarginata, Horberts cf. dianthus; 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; Iib.

*Bazzania trilobata (L.) Gray
Uncommon; bank on mire slope, Sphagnum compactum mesic mire; AT25-35, 115601; Alexai Point, Peaceful Valley; VIIb.

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), AT88-709, 115519, 124125A; this species was originally determined as Calycularia crispa 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-Sevent Hill; Copper Island (Bakalin & Cherdantseva 2008); Id (Note: distribution category corrected from le 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; Vlb.

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

Common; snowbed meadow, wet sedge meadow; ladyfern meadow, desiccated humus hole, *Phycomilum compactum* tuft; AT4-44, AT41-21, AT39-38, AT42-33, AT43-26, AT43-45, AT49-49, AT61-16, 115371 (mixed with *Pellia nepetina*), 115673, 115798 (mixed with *Diplophyllum albicans*), 115822 (mixed with *Lophozia* sp.), 115910 (mixed with *Saxtpania nigiformis*); 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. & Loske

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

**Cephalozia ambigu a** C. Massal. [Cephalozia bicupdita subsp. ambigu a (C. Massal.) R.M. Schust.]

Rare; alpine blueberry-crowberry meadow; AT33-43, 115244, Coast Artillery Hill; Bering Island (Bakalin 2005); Ila. Species separated from *C. bicupdita* 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. bicupdita* clade and probably it should be not separated on species level. But the whole *C. bicupdita* complex (*C. bicupdita* clade) is very complicated and needs further detailed study to clarify if the specific status of some taxa of this complex is correct.

**Cephalozia bicupdita** (L.) Dumort. (L.)

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*, *Kargia paniflora*), AT25-37 (JV), AT39-40 (mixed with *Calypogeia sphagnicola*), AT42-39 (mixed with *Calypogeia muelliriana*, *Saxtpania cf. irigya*, *Harpanthus florentianus*), AT42-40 (BS), AT60-21 (BS), AT61-28, AT62-61 (mixed with *Triphlophenia quinquidentata*), 115383 (BS), 115555, mixed with *Diplophyllum albicans*, *Gymnostema inflata*, *Narda saxalis*, *Barbthrophyles iuleti (IV)*, 115799 (mixed with *Diplophyllum albicans*), 115879 (BS), 115993 (mixed with *Gymnostema inflata*), 116161 (JV), 116170 (mixed with *Fuscocephaloziopsis albescens* IV), 116262 (BS); reported by Clark & Frye (1948), Evans (1900), Macoun (1902); Al-exai Point, Casco Point, Coast Artillery Hill, Lake Elwood, O'Donnell Valley, Robinson Ridge, Terrible Mountain, West Massacre Valley; Bering Island (Bakalin 2005); VII (bipolar).

**Cephalozia diversa** (Sm.) Schiff. [Cephalozia lyssaxea 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).

**Cephalozia varians** (Gottsch.) Steph.

Rare; damp area near stream, shaded damp humus of crevice; 116057A (JV), 116310 (BS); Murder Point, Peaceful Valley; Ila (bipolar).

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

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

**Chiloscyphus polyanthus** (L.) Corda

Uncommon; Nootka lupine alluvial meadow, mountain streamlet, edge of pond in wetland, bank above streamlet, alluvial meadow; 50-44 (mixed with *Conocephalum salicinum*), AT13-42, AT345, AT43-16, AT2006-50-44 (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** Szweyck., Bucz. et Odryzk.

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 meire, 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 *Sphagnum miniatum*), 115352, 120542, 120310A (BS), reported by Clark & Frye (1948, 1949), Frye & Clark (1946); Cape Wrangell, Casco Cove, Henderson River, Jarmin Pass, Massacre Bay, Peaceful Valley, Robinson Ridge, Tennae Cove, Terrible Mountain; Bering Island (Bakalin 2005); IIIc.

**Diplophyllum obsusfolium** (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.), 115512B, 115544B, 115552A, 115604, 116231 (mixed with *Triphlophenia quinquidentata*, *Maraspella emarginata*), 120506A; reported by Clark & Frye (1948, 1949), Persson (1952), Sharp & Hattori (1968); Casco Point, Nevidiskov Bay, Peaceful Valley, Thirty-Sevent Hill; Bering Island (Bakalin 2005); IVa.

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

[Diplophyllum imbricatum (M.A. Howe) Müller Frits.]

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

**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 meadow; AT21-27, AT22-30, AT24-27, AT103-29, 115586, 115691, 115952 (mixed with *Diplophyllum taxifolium*), 120170, 120301B, 120343; reported by Sharp & Hattori (1968); Beach Road, Casco Cove, Coast Artillery Hill, Gilbert Ridge, Terrible Mountain, West Mountains; Bering Island (Bakalin 2005); IIIc.
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*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. MH325700); Massacre Bay, Thirty-Seven Hill; IIb.

Fuscocephaloziopsis albenscens (Hook.) Váňa & L. Söderstr. [*Phleurocladula albenscens* (Hook.) Spruce] Rare; rock cliff outcrop, late snowbed meadow, cliff crevice, mesic mire, seepage streamlet; AT20-33, AT22-40, AT59-27 (mixed with *Anthelia jurataeiana*, AT60-13, AT414, AT477A, 116147, 116179 (mixed with *Moreckia lyttii*), 116265, 120172; reported by Davison (1993) from a collection of Sharp 9546 (TENN); Cape Wrangel, Coast Artillery Hill, Robinson Ridge, Terrible Mountain; Bering Island (Bakalin 2005); I.a.

Fuscocephaloziopsis lunulifolia (Dumort.) Váňa & L. Söderstr. [*Cephalozia lunulifolia* (Dumort.) Dumort.] Uncommon; shaded wall of gully, humus in maritime outcrop; mixed with *Kusza bicuspidata*, *Cephalozia bicuspitada*, *Diplyphyllum tzwolzolium*, 115677 (BS), 116313 (BS); reported by Clark & Frye (1949) as *Rare*; blowout in tundra; 116163 (JV); reported by Clark & Frye (1949), Sharp & Hattori (1968); Alexai Point, Murder Point; Bering Island (Bakalin 2005) and Copper Island (Bakalin 2010a); Iva.

Gymnocola inflata (Huds.) Dumort. Abundant; bog blueberry mire, submersed 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, 118949A, 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.

Gymnomitrion alpinum (Gottsche ex Husn.) Schinfl. [*Marsupella alpina* (Gottsche ex Husn.) Bernet] Reported by Persson (1968); IId.

Gymnomitrion brevissimum (Dumort.) Warnst. [*Marsupella brevissima* (Dumort.) Grolle] Rare; blowout in tundra; 116163 (JV); reported by Clark & Frye (1948) as *Gymnomitrion varians*; Robinson Ridge; Bering Island (Bakalin 2005); IId.

Gymnomitrion communatum (Limpr.) Schiffn. [*Marsupella communata* (Limpr.) Bernet] Reported by Davison (1993) from a collection of Sharp 9467 (TENN); IId.

Gymnomitrion concinnum (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 *Diplyphyllum albicans*) (BS), 116205, 116349, 120158, 120482; reported by Davison (1993) from a collection of Sharp 9404 (TENN); Coast Artillery Hill, Henderson River, Peaceful Valley, Robinson Ridge, Siddens Valley, Tenac Valley, Terrible Mountain, Thirty-Seven Hill; Bering Island (Bakalin 2005); Iia (bipolar).

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

Gymnomitrion obtusum Lindb. Uncommon; damp open cliff face, dry cliff, damp disturbed area; 115835 (BS), 115906 (BS), 116346 (mixed with *Diplyphyllum albicans*); reported by Clark & Frye (1949); *Coast Artillery Hill, Jinrin Pass, mouth of Peaceful River*; IIf (bipolar).

*Gymnomitrion pacificum* Grogle 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); Ile.

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

*Harpantus flavovianus* (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, Noooka lupine meadow; AT44-22, AT42-62, 116003 (mixed with *Scapania undulata*); 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 (Schofield et al. 2013), but this species was incorrectly separated from others in the past; apparently *H. aduncus* is not reported from the Commander Islands (Bakalin & Cherdandtscheva 2008), nor Bakalin (2010a). Ile.

***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 Jussev (2008), nor Bakalin (2010a). Ile.

*Herbertus dierensis* (Gottsche, Lindlb. & Nees) Trevis. Abundant; dump bank of small gully, reddish-rusty mats on dump outcrop of mountain slope, deeply shaded gully, dump outcrop face, seepage slope, intermittent streamlet in tundra, shaded wall of hole on slope, shaded wall of gully, 133

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, 120441; Alexei Point, Beach Road, Coast Artillery Hill, Henderson River, Jarmin Pass, Lake Edworth, Peaceful Valley, Temnac Cove, Terrible Mountain, Thirty-Seven Hill, West Mountains; unreported from the Commander Islands (Bakalin 2010a); Ilh. [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 *Mylia taylorii*); 115378, 115685, 115841, 116339, 120496; Alexei Point, Coast Artillery Hill, Temnac Cove, Terrible Mountain, Thirty-Seven Hill, West Mountains; unreported from the Commander Islands (Bakalin 2010a); Ilh. [AmphiPacific (disjunct Africa and India)].

**Hygrobiella 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); IIC.

*Jungermannia atroviens* Dumort.

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

*Jungermannia borealis* Damsh. & Váňa

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.) Váňa

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, 115956 (JV), 116271 (JV); Coast Artillery Hill, Gilbert Ridge, Terrible Mountain, Thirty-Seven Hill, USCG Lorcan C Station; Bering Island (Bakalin 2005 as *Jungermannia ericoidifolia* Schljakov); IIIa.

*Jungermannia pumila* With.

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

*Kurzia makinoana* (Steph.) Grolle

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

*Kurzia pauciflora* (Dicks.) Grolle

Rare; bank above stream, hard bank on mesic slope, peaty sod, shaded hole in slope; 115606A (BS), 115724, 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.
Liverworts from Attu Island, Alaska with comparison to the Commander Islands, Russia

Schuster (1980); Gilbert Ridge, Jarmin Pass, Bering Island, Bering Island (Bakalin 2005); VIIa.

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

*Porella farririi* (Steph.) S. Hatt. [P. vernicosa Lindb. subsp. farririi (Steph.) M. Haral]
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; VJe.

*Preissia quadra* (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 wenzeldii*); Peaceful Valley; VJe.

*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); VJe.

*Radula obtusiloba* (Steph.) S. Hatt, R. obtusiloba 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); Alexai Point, Gilbert Ridge, Beach Road, Cape Wrangell, Casco Point, Gilbert Ridge, Thirty-Seven Hill, Nevidiskov Creek, Terrible Mountain, West Mountains; Ve.

*Radula prolifer* 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 degemii* Schiffn. ex Müll. Frib. [Scapania brevianalis 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 Gymnocephale inflata) (BS & JV), AT42-28 (JV; mixed with *Cephalozia bicuspidata*), AT43-29 (mixed with *Cephalozia bicuspidata*, Trilophozia quinquidentata) (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), 115605 (mixed with Dichodontium pellucidum) (BS), 115749 (BS), 116010 (BS), 116032 (mixed with Diplophyllum allianum, 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); IIIb.

*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; IIIb.

*Scapania subalpina* (Nees ex Lindenh.) Dumort.
Rare; peaty stream bank, roadside ditch bank, alluvial valley, wet cliff; AT88-800, 115591 (mixed with *Cephalozia 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* (Lindb. subsp. ptilidii) (Steph.) L. Hampe
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, 115330, 115333, 115397, 115595A, 115635, 115662, 115794, 116562 (mixed with *Marsupella emarginata*), 116563 (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; IIIb.

*Scapania undulata* (L.) 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, 115330, 115333, 115397, 115595A, 115635, 115662, 115794, 116562 (mixed with *Marsupella emarginata*), 116563 (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; IIIb.

Liverworts from Attu Island, Alaska with comparison to the Commander Islands, Russia

Splenobolus minutus (Schreb. ex D. Cranitz) Berggr. [Anastrophyllum minutum (Schreb.) R.M. Schuster]

Common; damp outcrop, alpine blueberry heath, bank of humus hole in gully, cliff crevice, near water source, humus on cliff, seepage slope, bluejoint-alpine blueberry heath; 115626, 116241 (mixed with *Racomitrium lanuginosum*); Bering Island (Bakalin 2005); IVa.

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

Common; damp outcrop, alpine blueberry heath, bank of humus hole in gully, cliff crevice, near water source, humus on cliff, seepage slope, bluejoint-alpine blueberry heath; 115626, 116241 (mixed with *Racomitrium lanuginosum*); Bering Island (Bakalin 2005); IVa.

Trilophozia quinquedentata (Huds.) Bakalin [Tritomaria quinquedentata (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; 116256 (mixed with *Fuscosporangiopsis planifoliata*); reported by Clark & Frye (1948); Coast Artillery Hill, Peaceful Valley, Lake Elwood, Terrible Mountain, West Arm Nevidiskoy 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, or 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 1.2 %) (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 Tukkanen (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*, *Gymnozoon inflata*, *Herbertus dicranus*, *Marsupella emarginata*, *Nardia scalaris*, *Scapania uliginosa*, while common species were *Barbula nigricans*, *Blepharostoma triechophyllum*, *Calypogeia mulleri*, *Cephaloziella bicuspidata*, *Jungermannia excursifolia* subsp. *cordifolia*, *Lophozia longiflora*, Mylia *talhori*, Neorhizinae *florkei* and *Splenobolus 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): *Atrichum hyalinum*, *Barbula nigricans* butcheri, *Calypogeia integrifolia*, *Cephaloziella elachista*, *C. uminata*, *Conocephalum japonicum*, *Eremotrichum myriosporum*, *Fuscosporangiopsis leucaantha*, *Pachyuntia pachyantha*, *Jungermannia excursifolia* subsp. *excursifolia*, *L. polaris*, *Lophocolea heterophylla*, *L. minor*, *Lophozia saviczia*, *L. schutzeniana*, *L. silvicoloides*, *L. silvicoloides*, *Lophozia pelliculosa*, *Marsupella sprucei*, *Mesnỗia gillinii*, *M. heterocaulos*, *Mylia
Table 1. Percent distribution of Attu Island, Alaska, liverwort species in phytogeographic categories following the North Holarctic categories of Konstantinova (2000).

<table>
<thead>
<tr>
<th>Phytogeographic category</th>
<th>Number of species</th>
<th>Percent of flora</th>
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<tbody>
<tr>
<td>I. ARCTIC</td>
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</tr>
<tr>
<td>d. Siberian-American</td>
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<tr>
<td>II. ARCTOMONTANE</td>
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<tr>
<td>a. Circumpolar</td>
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<td>h. Eurasian-West American</td>
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<td>VIII. UNCLEAR</td>
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Table 2. Percent distribution of liverwort species in major North Holarctic elements (Konstantinova 2000) compared to Attu Island, Alaska (present study).

<table>
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<th>Geographic element</th>
<th>North Holarctic</th>
<th>Attu Island</th>
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<tr>
<td>Total</td>
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</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Commonness category</th>
<th>Number of species</th>
<th>Percent of flora</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rare</td>
<td>54</td>
<td>48.2</td>
</tr>
<tr>
<td>Uncommon</td>
<td>24</td>
<td>21.4</td>
</tr>
<tr>
<td>Common</td>
<td>11</td>
<td>9.8</td>
</tr>
<tr>
<td>Abundant</td>
<td>9</td>
<td>8.1</td>
</tr>
<tr>
<td>No data*</td>
<td>14</td>
<td>12.5</td>
</tr>
<tr>
<td>Total</td>
<td>112</td>
<td>100</td>
</tr>
</tbody>
</table>

* 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. flavum and L. stevensiana growing in admixture with Acerobolbus 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. flavum 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
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 dela-vaayi* 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, Tatetwaki (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 *Hulteria* as a link between the liverwort floras of Asia and America, and the Tatetwaki-line in dividing the Aleutian Islands from the Commander Islands is of great value in liverwort bryogeography (Bakalin & Cherdan seva 2008). For example, *Hulteria* may have served as a bridge between North America and Asia harboring relics of Cold and Warm Pleistocene epochs (Bakalin & Cherdan seva 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 *Hulteria* may play a significant role as a migration path for liverworts (Bakalin & Cherdan seva 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 relics 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.

**ACKNOWLEDGEMENTS**

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**LITERATURE CITED**


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**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).

<table>
<thead>
<tr>
<th>Region</th>
<th>Attu Island</th>
<th>Commander Islands</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total number of species</td>
<td>112</td>
<td>112</td>
</tr>
<tr>
<td>Number of Attu species present on Commander Islands</td>
<td>66 (59%)</td>
<td>absent on Commander Islands – 48 (41%)</td>
</tr>
<tr>
<td>Number of Commander species absent on Attu Island – 41 (37%)</td>
<td>present on Attu Island – 68 (59%)</td>
<td></td>
</tr>
</tbody>
</table>

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Talbot, S.S., S.L. Talbot & L.R. Walker 2010. Post-eruption legacy effects and their implications for long-term reco-


