VARIATION IN *LINNAEA BOREALIS* (LINNAEACEAE) ACROSS NORTH AMERICA AND GREENLAND

Peter F. Zika

WTU Herbarium, Box 355325
University of Washington
Seattle, Washington 98195, U.S.A.
zikap941@gmail.com

Gordon C. Tucker

EIU Herbarium, Dept. of Biological Sciences
Eastern Illinois University
600 Lincoln Ave., Charleston, Illinois 61920, U.S.A.
gctucker@eiu.edu

ABSTRACT

Three subspecies of *Linnaea borealis* (Linnaeaceae) are reported from North America. We reviewed the literature and herbarium specimens, and were able to consistently recognize two taxa in the herbarium and in nature. Floral characters distinguish the two subspecies. *Linnaea borealis* subsp. *borealis* is widespread across Eurasia, and is common in the Aleutian Islands and mainland Alaska. *Linnaea borealis* subsp. *longiflora* is represented in eastern and southeastern Alaska, south to California, and east to the Atlantic and Greenland, and includes plants called subsp. *americana*. PCA and statistical analyses support the recognition of two infraspecific taxa. Lectotypes are designated for *Linnaea borealis* var. *longiflora* and *Linnaea borealis* var. *longiflora* forma *orientalis*. Also, a neotype is chosen for *Linnaea americana*.

RÉSUMÉ

Trois sous-espèces de *Linnaea borealis* (Linnaeaceae) ont été signalées en Amérique du Nord. Nous avons examiné la littérature et les spécimens d'herbier, et nous avons pu reconnaître systématiquement deux taxons dans l'herbier et dans la nature. Les caractères floraux distinguent les deux sous-espèces. *Linnaea borealis* subsp. *borealis* est répandu à travers l'Eurasie, et est commun dans les îles Aleutian et le partie continental d'Alaska. *Linnaea borealis* subsp. *longiflora* est représentée dans l'est et le sud-est de l'etat d'Alaska, au sud de la Californie, et à l'est de l'Atlantique et du Groenland, et comprend des plantes appelées subsp. *americana*. Analyse des composantes principals et les analyses statistiques soutiennent la reconnaissance de deux taxons infraspécifiques. Les lectotypes sont désignés pour *Linnaea borealis* var. *longiflora* et *Linnaea borealis* var. *longiflora* forma *orientalis*. Aussi, nous avons choisi un néotype pour *Linnaea americana*.

INTRODUCTION

The genus *Linnaea* L. is circumboreal. Linnaeaceae is a recent segregate from the traditional, broader circumscription of Caprifoliaceae. Various segregate families (or reassignments) of taxa traditionally placed in Caprifoliaceae have been proposed (Jacobs et al. 2010), including the transfer of *Sambucus* L. and *Viburnum* L. to Adoxaceae, placement of *Diervilla* Mill. and *Weigela* Thunb. in Diervillaceae, placement of *Linnaea*, (as well as *Abelia* R. Br., *Diabelia* Landrein, *Dipelta* Maxim., *Kolkwitzia* Graebn., and *Vesalea* M. Martens & Galeotti) in Linnaeaceae, and retention of only *Lonicera* L., *Symphoricarpos* Duhamel, and *Triosteum* L. in a much more narrowly circumscribed Caprifoliaceae (Backlund & Pyck 1998). Christenhusz (2013) lumped all genera of Linnaeaceae in the genus *Linnaea*, but his approach was not taken up in subsequent molecular work (Landrein & Prenner 2016), nor by us. Alternatively, all these taxa except *Sambucus* and *Viburnum* might be included in Caprifoliaceae in the broad sense, along with Dipsacaceae and Valerianaceae, as a very broadly circumscribed Caprifoliaceae (Donoghue et al. 2001). However, the addition of the latter two families would result in excessive morphological diversity in Caprifoliaceae, in our opinion.

Familial placement notwithstanding, *Linnaea*, as a wide ranging genus, has been classified in various ways. Hultén (1930, 1937, 1949, 1968) presented maps and descriptions of three subspecies of *Linnaea borealis* L. in Alaska: subsp. *americana* (Forbes) Hultén, subsp. *borealis*, and subsp. *longiflora* (Torr.) Piper & Beattie. Other authors have preferred to place these taxa at the rank of varieties (Harrington 1954; Cronquist 1959; Abrams & Ferris 1960; Cronquist & Holmgren 1984; Gleason & Cronquist 1991; Ackerfield 2015; Gilman 2015) or to raise all three taxa to full species (Rydberg 1917; Pojarkova 2000).

Linnaea borealis is a self-incompatible, clonal subshrub, based on studies of subsp. *borealis* (as var. *borealis*) and subsp. *longiflora* (as var. *longiflora*) (Halverson 1986; Scobie & Wilcock 2009). The flowers bear nectar (Landrein & Prenner 2016) and are pollinated by bees and flies. Although twinflower produces abundant seed

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in some regions, e.g., Québec and the Cascade Range of Washington, it does not persist in the seed bank (Granstrom 1982).

METHODS

It is ironic that the genus named in honor of Linnaeus, the father of taxonomic botany, has never been the subject of a detailed evaluation of specific and infraspecific variation. We attempted to resolve these differing views of the classification of *Linnaea* as we prepare a treatment of the genus for the Flora of North America North of Mexico. Digital specimen images were viewed from ALA, BM, C, CGE, E, K, LINN, NY, PH, and S, in a search for North American types. We reviewed the literature and herbarium specimens at A, BM, CAS, CDA, CGE, DS, EIU, FR, GH, IA, ILL, ILLS, ISC, JEPS, KANU, LL, MO, MOR, NEBC, NY, ORE, OS, OSC, POM, RENO, RSA, SBBG, SD, TAES, TAMU, TEX, TEXA, UC, UPS, US, UTEP, V, VT, WILLU, and WTU. In addition, we examined populations in the field, in British Columbia, Idaho, Oregon, Washington, western Alaska, and in the Russian Far East. We assessed the discriminating morphological characters proposed by previous authors, especially Hultén (1968), who separated his three taxa using leaf shape, corolla shape, and the relative length of the sepals and the corolla tube. We evaluated these characters using herbarium material and from observations of living plants.

Floral measurements were taken from 162 herbarium specimens at EIU, FR, GH, ILL, NY, RSA, TEX, and WTU (Table 1). Our sample comprised 75 herbarium sheets from Eurasia and western Alaska, and included representative material of *Linnaea borealis* subsp. *borealis* from 14 countries. Another 87 sheets of *L. borealis* subsp. *longiflora* were included in the study from eastern and southeastern Alaska, North America and Greenland, covering 26 states and provinces. Herbarium sheets were chosen if they displayed at least one flower at full anthesis, pressed to clearly show the shape of the corolla and length of the sepals. On one flower per herbarium sheet we measured sepal length, corolla tube length, and converted these measurements to a ratio. We also measured the length and width of the expanded portion of the same corolla. Sepal length was measured from the base of the calyx to the tip of the longest sepal. The corolla tube length was measured from the base of the calyx to the inflection point, where the more or less parallel-sided corolla tube transitioned into a flaring corolla bell. The length of the expanded portion of the corolla was measured from the inflection point to the tip of the longest petal. Corolla width was measured as the widest point of the pressed flower. Analysis of data was made using "R: A Language and Environment for Statistical Computing" (R Core Team 2016) and Wickham (2009), with assistance from Daniel Tucker. We analyzed the contribution of two floral ratios in a PCA, using a linear mixed effects model (LMEM) comparison with maximal random effects structures. Random effects were assigned to location, and treated as a factor. The significance levels (p-values) reported below compare the maximal model in each case, against the same model minus the relevant parameter. All ratio measurement data was log-transformed and centered prior to analysis to respect the normality assumptions of LMEMs.

RESULTS

Foliage

Hultén (1968) used leaf shape to discriminate between subspecies. He attributed elliptical and acute leaves to *Linnaea borealis* subsp. *longiflora,* broadly ovate to roundish leaves "often somewhat acute" to subspp. *borealis* and *americana*. Rydberg (1907, 1917) used some foliage characters to cleave his taxa, such as the degree of toothing on the leaf margin, and if the leaves were broadest below, at, or above the middle. We quickly determined that the leaves varied from small to large, elliptical to ovate, obovate, or orbicular, toothed to entire, and acute to roundish, across the range of the species, and without discernible correlation to floral characters or geography. Even small samples, like those on a single herbarium sheet, could demonstrate wide variation (Fig. 1). Elliptical acute leaves, such as those said to be restricted to subsp. *longiflora* in North America, were found on a number of Eurasian specimens, e.g., Russia, *Kanz s.n.* (FR); Switzerland, *Weimer s.n.* (FR); and Sweden, *Müller-Haeckel s.n.* (FR). Environmental conditions can affect leaf size. Plants in windswept habitats, such as the maritime tundra of the Aleutians, tend to be smaller and to have smaller leaves, unless growing in sheltered

Table 1. Geographic coverage for floral samples of *Linnaea borealis* used in Fig. 4.

Subsp. *borealis*			Subsp. *longiflora*		
Country	N =	Region	N =	Region	N =
Austria	4	Alaska (eastern)	7	Minnesota	3
China	1	Alberta	3	New Hampshire	2
Denmark	2	British Columbia	5	New York	1
Finland	11	California	3	North West Territory	3
Germany	1	Colorado	2	Nova Scotia	1
Italy	1	Greenland	1	Oregon	4
Japan	3	Idaho	1	Québec	3
Norway	5	Illinois	1	Saskatchewan	3
Poland	1	Labrador	1	South Dakota	2
Russia	18	Mackenzie	1	Utah	1
Sweden	6	Maine	4	Washington	22
Switzerland	6	Michigan	4	Wisconsin	5
United Kingdom	1	Manitoba	2	Wyoming	2
United States (western Alaska)	15				
Totals	75				87

sites. Some appreciation of the diversity of leaf outlines can be found in Wittrock (1907), where more than 150 new forms of *L. borealis* were described and provided Latin names, some based on minor foliage differences. Among his proposed taxa were *Linnaea borealis* forma *microphylla* Wittr., forma *minutifolia* Wittr., forma *platyphylla* Wittr., forma *stenophylla* Wittr., and forma *subrotundifolia* Wittr. We agree with Wittrock and Hultén that there are many variations in leaf shape, but we were unable to find consistent foliage characters that were useful for distinguishing infraspecific taxa of *L. borealis*.

Calyx length

The absolute length of the calyx varies greatly across the range of the species. Fernald (1922) stated that sepals more than 3 mm long were restricted to *Linnaea borealis* subsp. *longiflora* (as var. *longiflora*), while sepals from 1.5–3 mm were found in both subsp. *borealis* (as var. *borealis*) and subsp. *americana* (as var. *americana*). We found sepals as short as 1 mm in Greenland samples of subsp. *longiflora*, and occasional subsp. *borealis* plants in Eurasia with sepals up to 3.5 mm long, e.g. Finland, *Wehrmeyer s.n.* (FR); Norway, *Schrenk 6* (FR); and Sweden, *Müller-Haeckel s.n.* (FR). Long or short sepals were observed from all across North America; thus, we do not regard sepal length as significant or associated with geography. However, the relative length of the corolla tube and sepals is more meaningful.

When the length of the calyx was compared to the length of the corolla tube, we found a useful means to sort specimens, correlated to geography. In *Linnaea*, the corolla is cylindrical proximally, resembling a straight-sided tube of variable length, then expands or flares upward into a bell or funnel shape. We refer to the basal, cylindrical portion of the corolla as the corolla tube. In Eurasian material, subsp. *borealis*, the corolla tube is generally obscured by the calyx, because the free tips of the sepals are longer than the corolla tube (Fig. 2A). With the exception of some Alaskan material that matches subsp. *borealis*, the remainder of North American collections have a corolla tube that equals or exceeds the sepal tips. This is easily observed in the field on mature flowers at anthesis (Fig. 2B). Developing, immature, or poorly pressed flowers may appear to have a floral tube shorter than the sepals, but the vast majority of corollas seen fresh have elongated tubes in North America. Conversely, flowers seen in the field in eastern Russia and the Aleutian Islands had abbreviated tubes.

Corolla shape: short wide flowers

Hultén (1968, p. 843) distinguished between *Linnaea borealis* subsp. *borealis* and subsp. *americana* based on the corolla shape. He said that subsp. *americana* was "similar to subsp. *borealis*, but corolla more funnel-shaped, with tube flaring from above calyx." We agree with Hultén, after examining many hundreds of collec-

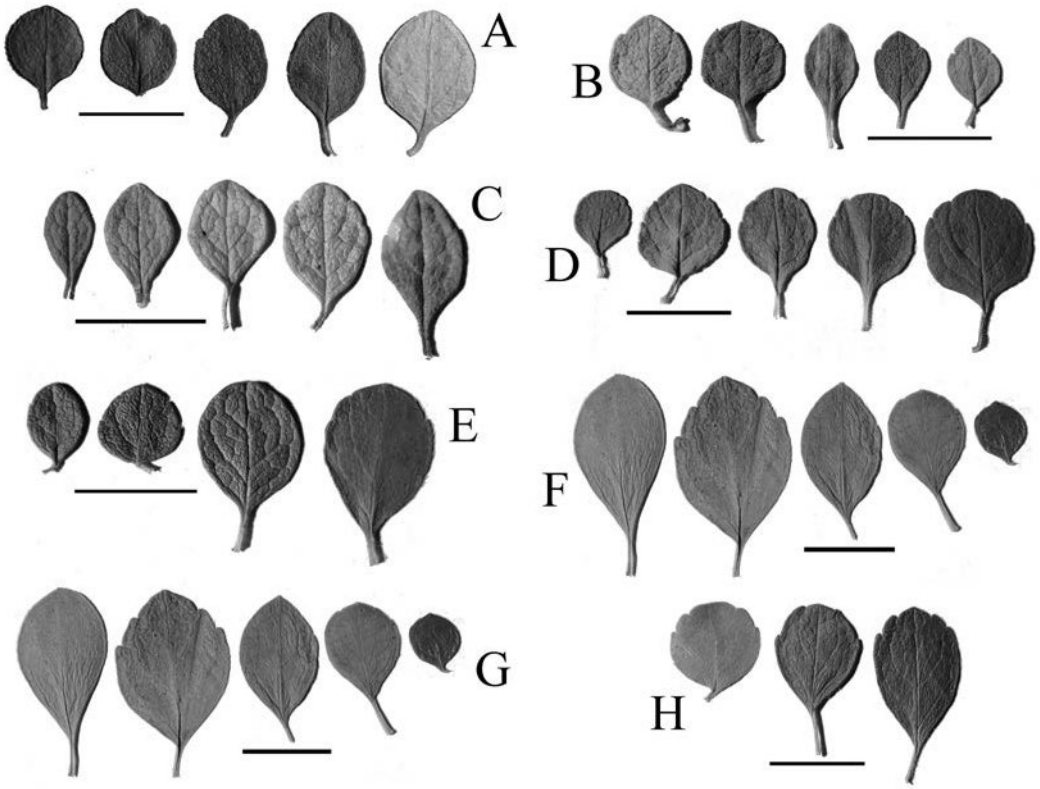

Fig. 1. Leaf variation in *Linnaea borealis*. A–D. Subsp. *borealis*, leaves orbicular to elliptic, ovate, or obovate, margins entire or toothed, apices rounded to acute. **A.** Anchorage, Alaska (*Zika 26687*). **B.** Unalaska Island, Aleutian Islands, Alaska (*Zika 26707*). **C.** Kurile Islands, Russian Far East (*Bakalin 6731*). **D.** Fedora Bay, Russian Far East (*Bakalin 6740*). E–H. Susbp. *longiflora*, leaves orbicular to elliptic, ovate, or obovate, margins entire or toothed, apices rounded to acute. **E.** Pend Oreille County, Washington (*Zika 26868*). **F.** Thurston County, Washington (*Zika 26544*). **G.** Skamania County, Washington (*Zika 26680*). **H.** Stevens County, Washington (*Zika 26836*). Scale bars 1 cm.

Fig. 2. Relative length of corolla tube and calyx in fresh *Linnaea borealis*. **A.** Subspecies *borealis*. Corolla tube is abbreviated and obscured by the calyx; sepal tips cover the base of the expanded portion of the flower. Attu Island, Aleutian Islands, Alaska. **B.** Subspecies *longiflora*. Corolla tube is elongated and exceeds the calyx; sepal tips are distant from the expanded portion of the flower. Washington State.

tions, that the Eurasian and Aleutian plants have a distinctive corolla shape, and it differs from the remaining North American plants. While this shape may be distorted in poorly pressed flowers, it is readily recognized in most material. These plants are the same as the type material of subsp. *borealis* illustrated by Jarvis (2007). Nomenclaturally typical plants have flowers that are generally as wide as long, or wider than long, if measured from the inflection point at the summit of the corolla tube. The margins of the bell-shaped, distal portion of the corolla can be slightly concave, straight-sided, or slightly convex on the same specimen, e.g. Switzerland, *Simon s.n.* (FR 65433), but often are slightly convex when seen in the field. We illustrate several pressed examples in Fig. 3A. The tips of the corolla lobes can be blunt or acute in Eurasian material, as in North American populations.

Corolla shape: long narrow flowers

In contrast to Eurasian collections, plants of eastern Alaska, southeastern Alaska, British Columbia and the Pacific states south to California had flowers clearly longer than wide, sometimes almost twice as long as wide (Fig. 3B–C). As noted by Cronquist (1959), the corolla shape varies to the east in North America, but most flowers are longer than wide. Long narrow corollas also have a relatively long tube, compared to the length of the sepal tips, as discussed above.

Floral ratios

We used a Principle Components Analysis (PCA) to analyze sepal to tube ratio and floral length to width ratio (Fig. 4). Eurasian specimens had flowers with short tubes and relatively wide corollas, and clustered together with plants from western Alaska, including the Anchorage area and all of the Aleutian Islands. Plants from eastern Alaska and southeastern Alaska, and east across North America to Greenland, were separable with relatively longer floral tubes, which correlated with their relatively longer and narrower corollas. Means and standard error are provided in Fig. 5 for our data.

DISCUSSION

Linnaea borealis subsp. *borealis* has a limited distribution in North America, entirely within Alaska. Corollas with the tube shorter than the sepals, and flowers as wide as long, are found in the Aleutian Islands, they are common in the Anchorage area, and there are scattered specimens from along the western mainland coast and across much of the interior of Alaska, but no vouchers were seen inland as far as the Yukon Territory. Reports of subsp. *borealis* from British Columbia (Douglas et al. 1998) are misidentifications of subsp. *longiflora*.

Linnaea borealis subsp. *longiflora* was accepted in the Flora of the Pacific Northwest (Cronquist 1959), and by Cronquist and Holmgren (1984) in the Intermountain Flora. They included Hultén's concept of subsp. *americana* as a synonym of subsp. *longiflora*, and we concur with them: "The material from western North America often shows the differences from typical var. *borealis* in more pronounced fashion than does the material from eastern North America, but no further taxonomic segregation seems reasonable" (Cronquist 1959). None-the-less, the epithet *americana,* at the rank of var. or subsp., is used in a number of North American floras, such as Fernald (1950), Harrington (1954), Harris et al. (1964), Moss and Packer (1983), Cooperrider (1995), Elven (2011), and Haines (2011).

Hultén's (1968) range maps showed subsp. *borealis* in the Aleutians, most of mainland Alaska except the southeastern coast, and throughout northern Eurasia. He mapped subsp. *americana* as overlapping subsp. *borealis* in most of Alaska, except the western-most mainland and in the Aleutians. His concept of subsp. *americana*, as shown by his range maps, included most plants of North America, and all the plants of Canada, Greenland, and the continental United States, with the exception of plants along the coast in the Pacific Northwest. Hultén (1968) separated populations from southeastern Alaska south to California as subsp. *longiflora*.

Our LMEM analyses revealed a robust main effect of the ratio of the longest sepal to the floral tube ($p < 0.01$), as well as a marginal main effect of the ratio (length:width) of the corolla bell ($p = .05$). Both ratio measures demonstrated significant explanatory power in subspecies differentiation, lending quantitative support to our claims. Neither our statistical nor our morphological data support Hultén's (1968) recognition of three

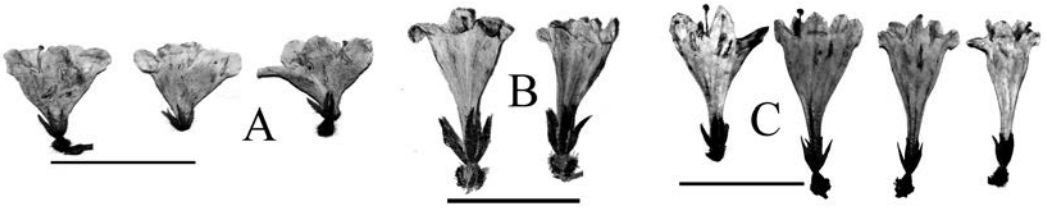

Fig. 3. Relative length of corolla tube and calyx in dried *Linnaea*. A. Subspecies *borealis*. Corolla tube is abbreviated and obscured by the calyx; sepal tips cover the base of the expanded portion of the flower. Fedora Bay, Russian Far East (*Bakalin 6740*). B–C. Subspecies *longiflora*. Corolla tube is elongated and exceeds the calyx; sepal tips are distant from the expanded portion of the flower. Washington State B. (*Zika 27022*). C. (*Zika 26746*). Scale bars 1 cm.

taxa for North America. When his concept of subsp. *americana* is combined with subsp. *longiflora* (Fig. 4), the result is a more harmonious classification that correlates geography and floral morphology in a sample across Eurasia, eastern and western North America, and Greenland. The situation in Alaska remains interesting and incompletely resolved. However, all populations from forested southeastern Alaska are subsp. *longiflora*. All material from the Aleutians, a windswept maritime tundra, and coastal collections from western Alaska (north of the panhandle) are subsp. *borealis*. As Hultén (1937, 1949, 1968) suggested, interior Alaska appears to represent a transition between Eurasian influence, subsp. *borealis*, and North American populations, subsp. *longiflora*. We do not follow Hultén's (1968) concept of treating somewhat intermediate plants as a distinct subsp. *americana*. Better herbarium material, with numerous well-pressed flowers, would help in better defining the distribution of the two accepted subspecies in interior Alaska. Most collections we saw were difficult to assess, with very few flowers and these were often poorly preserved and folded or wrinkled.

More than 20 different species of flies and bees were documented transfering *Linnaea* pollen in New Brunswick (Barrett & Helenurm 1987), Scotland (Scobie & Wilcock 2009), and China (Zhang et al. 2014). It would be interesting to know if there is a suite of different pollinators driving observed differences in corolla shape, with a comparative study in Alaska and adjacent territories.

TAXONOMY

Linnaea borealis L., Sp. Pl. 2:631. 1753. Type: [SWEDEN. Lapland journey, May 1732, *C. Linnaeus s.n.*], Herb. Linn. no. 250 (lectotype, designated by Jonsell (1993): library of Institut de France, Paris [image of flowering specimen in Jarvis (2007), who notes the locality is likely near Gävle, in Gävleborg County, between Uppsala and Umeå].

Subshrubs. **Stems** procumbent, pubescent, to 1 m long, often rooting at nodes, producing short, sub-erect, usually flowering stems to 10 cm tall. **Leaves:** petiole 2–5 mm long; blade (2–)6–27 mm long, (1.8–)5–22 mm wide, subcoriaceous, evergreen, margins entire to sparsely crenate (0–3 teeth per side), ciliate, abaxially glabrous (sometimes with a few hairs basally), adaxially sparsely pubescent, primarily near the margins. **Inflorescence:** erect slender axillary peduncles (3.5–)4–7(–10) cm, terminating in (1–)2(–4) opposite (or sub-opposite to alternate) pedicels and flowers, with 2 (rarely 4+) opposite (or sub-opposite) lanceolate (to oblong-elliptic) bracts at apex; pedicels 2–25 mm, with two glandular ovate bractlets at apex, ± enclosing or at least clasping ovary and fruit. **Flowers:** sepals lanceolate, finely pubescent, 1.5–5 mm; corolla white, tinged and striped rose-purple, or entirely pinkish, 6–16 mm, campanulate or funnelform, lobes acute or blunt, slightly spreading or not, 1.2–2 mm, the tubular portion shorter to longer than the calyx, glabrous or glabrate externally, pubescent within; anthers 1.2–1.7 mm; style slightly exserted; stigma capitate. **Fruits** 2–3.5 mm, elliptic to narrowly ovate, appressed-pubescent, yellowish, green, purple or brown. **Seeds** 1–2.5 mm, elliptic to narrowly ovate, yellowish or greenish.

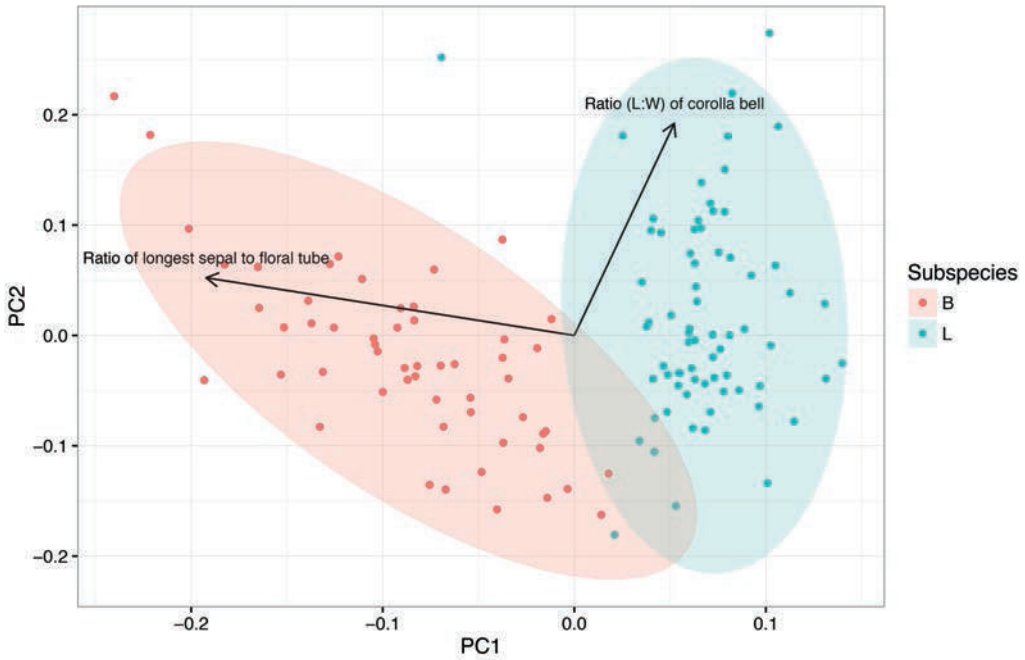

Fig. 4. PCA comparison of floral characters in *Linnaea borealis* subsp. *borealis* and subsp. *longiflora*. The graph is a visualized principle components analysis with normalized clusters for each of the two subspecies and eigenvectors showing the magnitude of each of the two ratio's contributions. Flowers with relatively short sepals and long narrow corollas cluster as *L. borealis* subsp. *longiflora*, in North America and Greenland. Flowers with relatively long sepals and short wide corollas cluster as subsp. *borealis*, from western Alaska and Eurasia.

KEY TO SUBSPECIES OF *LINNAEA BOREALIS*

1. Sepal tips equaling or longer than floral tube, expanded portion of corolla (above floral tube) usually wider than long; Eurasia (not in Greenland or Iceland), western Alaskan mainland and the Aleutian Islands _____ **L. borealis** subsp. **borealis**
1. Sepal tips shorter than floral tube, expanded portion of corolla (above the ± straight-sided basal floral tube) usually longer than wide; North America, including the Alaskan Panhandle and eastern Alaska (not in the Aleutian Is.), south to California and east to Greenland _____ **L. borealis** subsp. **longiflora**

Linnaea borealis L. subsp. **borealis**

Linnaea serpyllifolia Rydb., J. New York Bot. Gard. 8:135. 1907. TYPE: U.S.A. ALASKA: Cape Nome, summer 1900, *F.E. Blaisdell s.n.* (HOLOTYPE: NY 278497!; ISOTYPES: GH!, UC 112949!, US 421389!).

Subshrubs or vines. **Stems** procumbent, trailing, to 1 m. **Leaves:** blades roundish or obovate, usually ciliate and with few scattered hairs adaxially. **Flowers:** sepals (1.5–)2–2.6(–3.5) mm (usually longer than tubular portion of corolla); corolla (6–)8–11 mm, campanulate, the tubular portion as long as (or slightly shorter than) the calyx. $2n = 32$.

Flowering May–Aug. Open or dense conifer forest, peatlands, shores, moist to dry tundra, mossy or rocky slopes, fellfields, and open shrubby wetlands; 0–1200 m; Alaska; northern Europe, northern and northeastern Asia.

Linnaea borealis L. subsp. **longiflora** (Torr.) Piper & Beattie, Fl. N.W. Coast, 338. 1915, not Hultén 1937. *Linnaea borealis* L. var. *longiflora* Torr., U.S. Expl. Exped. 17:327. 1874; *Linnaea longiflora* (Torr.) Howell, Fl. N.W. Amer. 1:280. 1900. TYPE: [U.S.A. WASHINGTON: Pierce Co.: near Fort Nisqually, ca. 11–19 May 1841], Nasqually [sic], 1838–1842, *Wilkes South Pacific Exploring Expedition 139* [collected by either C. Pickering or W.D. Brackenridge] (LECTOTYPE, designated here: NY 278495! ex herb. Torrey; possible undated isolectotype: Puget Sound, *Wilkes Exploring Expedition 137* US 95392!). **Fig. 6.**

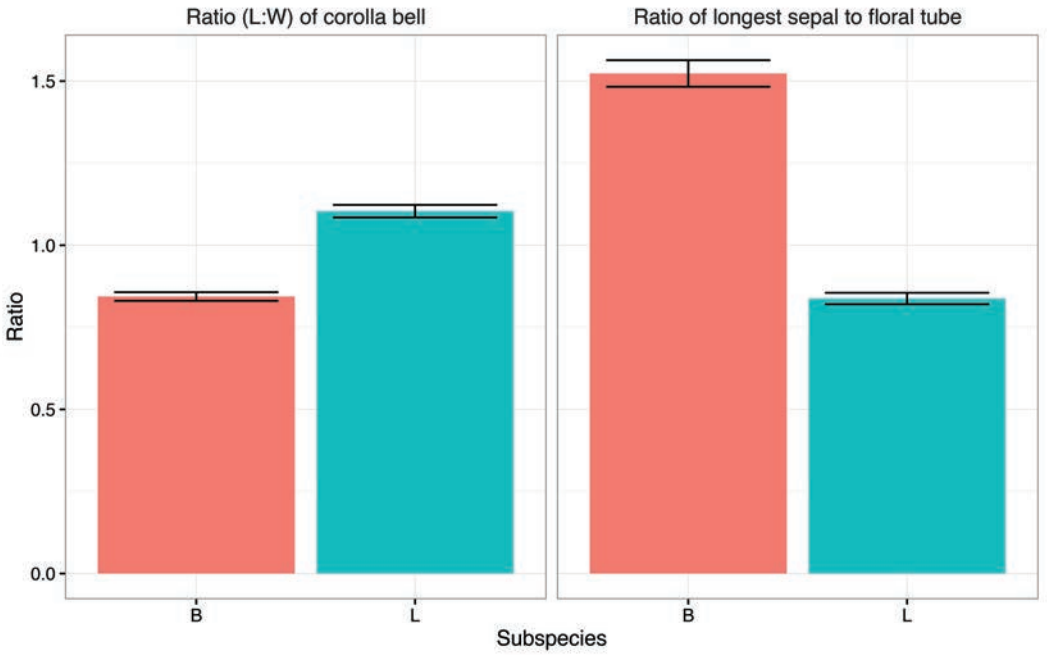

Fig. 5. A summary of the mean ratios for each subspecies of *Linnaea borealis*, with error bars showing standard error of the mean. N = 75 for subsp. *borealis*; N = 87 for subsp. *longiflora*.

Linnaea americana J. Forbes, Hort. Woburn. 135. 1833; *L. borealis* L. var. *americana* (J. Forbes) Rehder, Rhodora 6:56. 1904; *Linnaea borealis* subsp. *americana* (J. Forbes) Hultén, Fl. Aleut. Isl. 310. 1937. Type: CANADA. NOVA SCOTIA: [possibly near Halifax, where Menzies was posted 1784–1786] *A. Menzies s.n.* (Neotype, designated here: CGE 19999!, ex herb. Lindley, uppermost two plants on a sheet with four gatherings); isoneotype: LINN 1077.1, internet image! [dated 1784, two flowering plants in the upper left, labeled number two on a sheet with four gatherings]. **Fig. 7.**

Linnaea borealis L. forma *curticalyx* Wittr., Acta Horti Bergiani 4:174, Tab. 13, Fig. 13. 1907. Type: U.S.A. COLORADO: [Larimer Co.: Front Range], swamp above Beaver Creek, 9500 [–12000] feet, [2895–3660 m, Comanche Peak Wilderness], 7 Jul 1896, *C.S. Crandall 2062* (holotype: UPS V–730869!; isotype: NY 2435511, internet image!).

Linnaea borealis L. forma *integerrima* Wittr., Acta Horti Berg. 4:174, Tab. 13, Fig. 15. 1907. Type: CANADA. ALBERTA: Sheep Mountain, Waterloo Lake, latitude 49°5'N, 28–31 Jul 1895, *J. Macoun 10805* (holotype: C 10021722, internet image!).

Linnaea borealis L. forma *minutifolia* Wittr., Acta Horti Berg. 4:174, Tab. 13, Fig. 14. 1907. Type: U.S.A. VERMONT: [Franklin Co.], Highgate, 17 Jun 1838, *E. Tuckerman s.n.* (holotype: UPS V–730812!).

Linnaea borealis L. var. *longiflora* Torr. forma *angustissima* Wittr., Acta Horti Berg. 4:173, Tab. 13, Fig. 12. 1907. Type: U.S.A. [WASHINGTON: Skagit Co.], Fidalgo Island, Oregon Boundary Commission, 1858, *Dr. D. Lyall s.n.* (holotype: UPS V–730871!; isotypes: CGE!, GH! ex herb. John Ball; K 1092816 ex herb. Hooker internet image!).

Linnaea borealis L. var. *longiflora* Torr. forma *insularis* Wittr., Acta Horti Berg. 4:173, Tab. 13, Fig. 11. 1907. Type: CANADA. BRITISH COLUMBIA: Plants of Vancouver Island, District of Renfrew, growing in salal underbrush, Jun–Jul 1901, *C.O. Rosendahl & C.J. Brand 20* (holotype: UPS V–730870!; isotypes: BM 1191401!, C 10021721 internet image!, DS 19763!, K 1092819 internet image!, NY 2435624 internet image!, POM 59801!).

Linnaea borealis L. var. *longiflora* Torr. forma *orientalis* Wittr., Acta Horti Berg. 4:173, Tab. 13, Figs. 7–10. 1907. Type: U.S.A. [NEW HAMPSHIRE: Coos Co.: Presidential Range, White Mountains], alpine regions on the sides of Mounts Pleasant [now Mt. Eisenhower] and Monroe, 6 Aug 1838, *E. Tuckerman s.n.* (Lectotype, designated here: UPS V–730840!; isolectotype: S). **Fig. 8.**

Subshrubs or vines, procumbent, trailing, to 1 m. **Leaves:** blades slightly larger, sparsely ciliate to nearly glabrous. **Flowers:** sepals (1–)3.2–4.5(–5.4) mm (usually shorter than the tubular portion of the corolla); corolla funnelform, (7–)10–14(–16.5) mm, the tubular portion longer than the calyx (expanded portion of corolla campanulate to funnelform). $2n = 32$.

Flowering May–Jul(–Aug). Dry to moist coniferous or deciduous forest and forest edges, peatlands, mossy

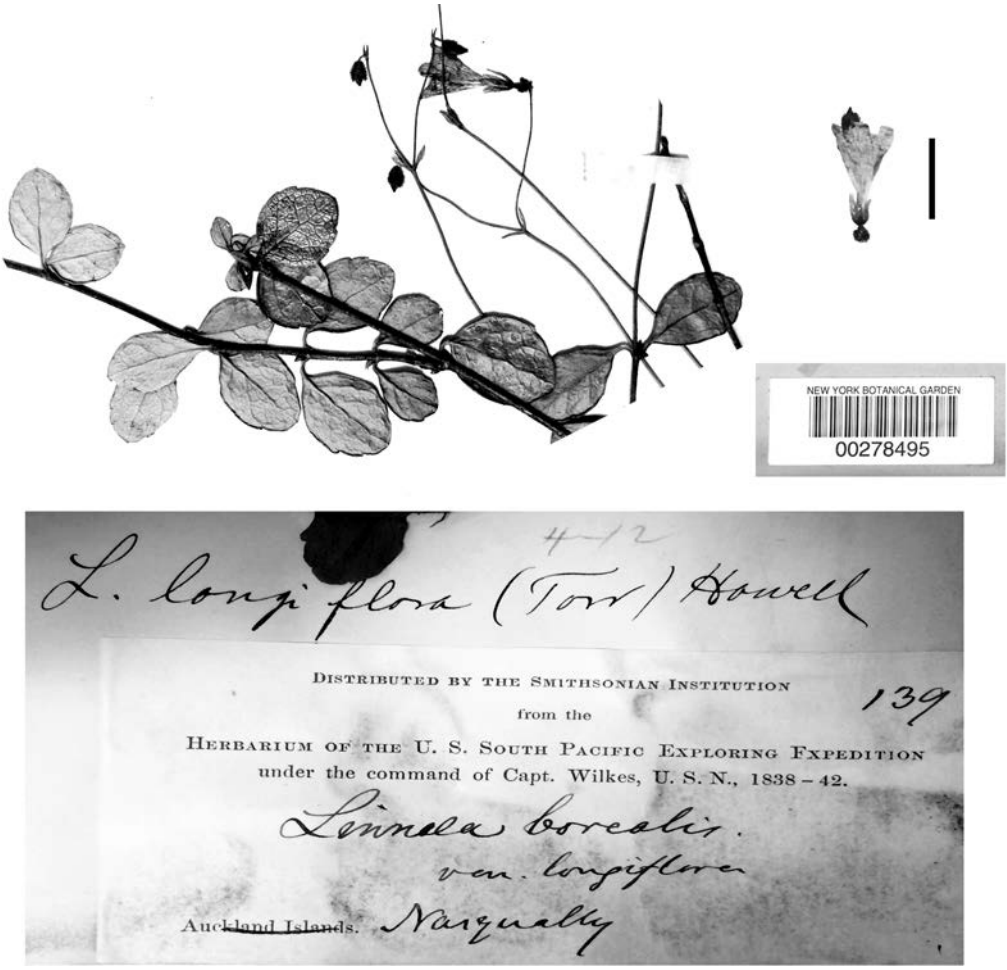

Fig. 6. Lectotype designated in this paper for *Linnaea borealis* var. *longiflora*, Washington, *Wilkes Exploring Expedition 139* (NY 278495). Reproduced with permission, this image belongs to The C.V. Starr Virtual Herbarium, The New York Botanical Garden (http://sweetgum.nybg.org/science/vh/). Scale bar 1 cm.

logs, gravelly, sandy, or rocky shores and slopes, subalpine to alpine meadows, clearings, roadsides; 0–2000(–3200) m; Greenland; St. Pierre & Miquelon; Alta., B.C., Man., N.B., Nfld. and Labr., N.W.T., N.S., Nunavut, Ont., P.E.I , Que., Sask., Yukon; Alaska, Ariz., Calif., Colo., Conn., Idaho, Ill., Ind., Iowa, Maine, Md., Mass., Mich., Minn., Mont., N.H., N.J , N.M., N.Y., N.Dak., Ohio, Oreg., Pa., R.I., S.Dak., Tenn., Utah, Wash., W.V., Wis., and Wyo.

Notes on typification

The following notes provide context for our neotype and lectotype selections. We list syntypes and original material so that unidentified duplicates may be more easily recognized in additional herbaria.

Linnaea americana (Fig. 7)

Forbes surviving collections and types are at K (Stafleu & Cowan 1976). His protolog (Forbes 1833) notes the species was introduced from "America" and cultivated in the gardens of Woburn Abbey, Bedfordshire, England, in the year 1800, but he failed to mention a collector, date, or provenance. Although we had the assistance

Fig. 7. Neotype designated in this paper for *Linnaea americana*, Nova Scotia, *A. Menzies s.n.* (CGE 19999); image reproduced with permission from Cambridge University Herbarium.

Fig. 8. Lectotype designated in this paper for *Linnaea borealis* var. *longiflora* forma orientalis, New Hampshire, *E. Tuckerman s.n.* (UPS V–730840); image reproduced with permission from Uppsala University Herbarium. Scale bar 1 cm.

of the keepers at Kew, we were unable to locate a pre-1800 Forbes collection that would represent his original material at the time of his description of *Linnaea americana*. So we have selected as a neotype a CGE specimen collected in Nova Scotia by Archibald Menzies in the mid-1780s. At the time, Menzies was an assistant-surgeon in the Royal Navy, and was posted in Halifax, Nova Scotia. In addition to his medical duties, he was procuring seeds and specimens for cultivation by Joseph Banks at K, and it is possible Menzies' living materials were eventually distributed by horticulturalists to institutions like Woburn Abbey. A non-flowering specimen at E, stamped 1854 from Bentham's herbarium, bears a collection dated 16 Sep [18]27 and labeled "Hort Edin[burgh?]" and "Linnaea borealis var. Americana." This suggests the possibility of further distribution of American material from Banks, Kew or from Forbes to select gardens in the British Isles.

***Linnaea borealis* var. *longiflora* (Fig. 6)**

Our review of the North American literature did not yield a lectotype designated for Torrey's trinomial, *Linnaea borealis* var. *longiflora* (Howell 1900; Piper 1906; Brenner 1908, 1910; Piper & Beattie 1915; Fernald 1922; Hultén 1937, 1949, 1968; Cronquist 1959; Abrams & Ferris 1960; Cronquist & Holmgren 1984). Torrey's (1874) protolog provided the following data: " Hab. Oregon, and northward to British Columbia and Sitcha [sic], eastward to the Rocky Mountains... In Lyall's, E. Hall's and other specimens from Oregon and Washington Territory, this character holds good; while at Fraser River an intermediate form occurs. From Utah and the Rocky Mountains only the ordinary form has been collected." Original material available to Torrey at the time of publication in 1874 would include the syntypes at GH, NY, PH, and US (see below), with duplicates elsewhere.

Torrey and Gray (1838–1841) also viewed David Douglas and John Scouler collections from the Pacific Northwest when visiting the herbaria of Banks, Hooker, Bentham, and others in Europe. We considered pre-1874 specimens from Oregon, Washington, British Columbia, and Alaska, including Sitka, but we eliminated Fraser River and Rocky Mountain collections based on Torrey's 1874 protolog. We considered gatherings by David Lyall, Elihu Hall, and other collectors, following Articles 9.2, 9.3, 9.5, and 9.12 of the Melbourne Code, as well as its Recommendation 9A.2 (McNeill et al. 2012). From the syntypes we chose a lectotype from the U. S. government's Exploring Expedition under the command of Lieutenant Charles Wilkes, in 1841 (Wilkes 1844). Torrey (1874) was summarizing the floral findings of Wilkes' Expedition when he described *Linnaea borealis* var. *longiflora* **(Fig. 6).**

Syntypes: U.S.A. ALASKA: U. S. Coast Survey, Sitka, 1867, *A. Kellogg 84* CAS!, DS!, UC!, US 57358, internet image! [Larsen's Bay, Kodiak Island, is given as the locality by Hultén (1949), who cites Durand (1869), but a US sheet (57358, internet image!) is numbered 84 and labeled Sitka, and the floral morphology (subsp. longiflora) is right for Sitka, in southeastern Alaska, and does not match subsp. borealis, expected on Kodiak Island. A second US sheet (57359, internet image!) is labeled "A. Kellogg 84" and "Larsen's Bay" but lacks corollas; it is not a syntype]. OREGON: 1869, *Miss Dorothea L. Dix s.n.* (NY 278494! [received by J. Torrey Apr 1871]); 1871, *Elihu Hall 222* (BM!, BRU 5906 ex herb. Olney, internet image!; BRU 5917 ex herb. Bennett, internet image!; NY 2435403 ex herb. J.H. Redfield, ex herb. Princeton, internet image!; NY 2435474 ex herb. Columbia College of Pharmacy, internet image!; NY 2435534, ex herb. J.J. Crooke, ex herb. N.L. Britton, internet image!; POM 297610!); [Multnomah Co.], Portland, 1868–1869, *Dr. A. Kellogg 335 & W.G.W. Harford* (BM!, NY 2435402 ex herb. J.H. Redfield, ex herb. Princeton University, internet image!). WASHINGTON: Cascade Mountains, 49° north latitude, Oregon Boundary Commission, 1859, *Dr. D. Lyall s.n.* (GH! ex herb. Royal Botanical Gardens Kew); [Clark Co.], Fort Vancouver, Washington Territory, 1854, *Major Alvord s.n.* (NY 278496!, ex herb. Torrey); [Pierce Co.], Steilacoom, plants collected in Washington Territory by the U. S. Pacific Railroad Survey under Isaac Stevens, 1853–1855, Jun, *Dr. J.G. Cooper s.n.* (US 227477, internet image!); [Skagit Co.], Fidalgo Island, Oregon Boundary Commission, 1858, *Dr. D. Lyall s.n.* (CGE!, GH! ex herb. John Ball, K 1092816 ex herb. Hooker internet image!, UPS V–730871!).

Linnaea borealis var. *longiflora* forma *orientalis* (Fig. 8)

Syntypes: [U.S.A. MICHIGAN: Chippewa Co.: near White Fish Point], Lake Superior, [19 Jun 1820, Cass Expedition (Torrey 1822; Shear & Stevens 1921, p. 151; annot. by R.L. Stuckey 1978)] *D.B. Douglass s.n.* (PH, ex herb. J. Torrey, internet image!). Lake Superior, Flora of North America, Torrey & Gray [the Torrey and Gray flora was published 1838–1841], [undated, anon. duplicate of the previous?], *s.n.* (UPS V–730801!, ex herb. A. Gray).

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