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Six indigenous species of Luzula, subgenus Anthelaea Griseb., are recognized in North America, viz. Luzula divaricata S. Wats., L. gigantea Desv., L. hitlecockii Hämet-Ahti, L. parviflora (Ehrh.) Desv., L. piperi (Goy.) M. E. Jones, and L. wahlenbergii Rupr. L. glabrata (Hoppe) Desv., which is commonly reported from western North America, is shown to be restricted to Europe; the American taxon usually presented under that name is described as a new species, L. hitlecockii Hämet-Ahti. L. parviflora has three major races in North America, viz. ssp. fastigiata (C. Meyer) Hämet-Ahti, n. comb., ssp. melanocarpa (Michx.) Hämet-Ahti, n. comb., and ssp. parviflora.

The genus Luzula DC. is divided into four subgenera, viz. Luzula, Pterodes Griseb., Anthelaea Griseb., and Marlenia Ebing. (cf. Buchanan 1906, Vierhapper 1930, Ebing 1963). The subgenus Anthelaea may be characterized as follows: perennial, espite to stoloniferous, inflorescence a panicle or a much branched corymb, and seeds without distinct caruncle. It contains at least 20 species, which chiefly occur in Eurasia and North America.

There are 6 indigenous species of this subgenus in North America, viz. Luzula divaricata S. Wats., L. gigantea Desv., s. lat., L. hitlecockii Hämet-Ahti, L. parviflora (Ehrh.) Desv., s. lat., L. piperi (Goy.) M. E. Jones, and L. wahlenbergii Rupr. In addition to these, a European species, L. albida (Hoffm.) DC. [L. luzuloides (Lamb.) Dandy & Wilmott, L. nemorosa (Poll.) E. Meyer], is naturalized in southeastern Canada and the northeastern U.S.A.

Key to the taxa treated

1. Perianth segments usually 2.5 – 3 mm long, dark brown to brown; anthers 1.2 – 1.5 mm long; capsule 2.5 – 3.5 mm long, ovate with up to 1 mm long beak
   2. Perianth segments usually shorter than 2.5 mm; anthers shorter than 1 mm; capsule shorter than 2.5 mm, elliptical or rounded but never ovate, beak short or indistinct
   3. Stolons long; perianth segments long-acuminate, clearly exceeding capsule
   4. Plants usually less than 30 cm tall; cauline leaves 2 – 3, up to 0.5 mm wide; bracts and bractlets strongly long-ciliate
   5. Cauline leaves 2, lanceolate, fairly thin, more or less shiny, green; lowest bract 0.4 – 1.0 cm long; seeds dark brown
   6. L. wahlenbergii
   7. Cauline leaves 3, linear, thick and dull, bluish to greyish green; the lowest bract 1.5 – 2.5 cm long; seeds pale yellowish brown
   8. L. piperi

2. Perianth segments usually 2.5 – 3 mm long, dark brown to brown; anthers 1.2 – 1.5 mm long; capsule 2.5 – 3.5 mm long, ovate with up to 1 mm long beak

3. L. hitlecockii

4. Plants usually less than 30 cm tall; cauline leaves (3 – 4) or more, 5 – 10 mm wide; bracts entire to slightly ciliate, bractlets entire to lacerate but never strongly ciliate

5. Inflorescence rich in flowers, with long major branches and with short ultimate branchlets; bracts and bractlets entire to slightly lacerate; perianth segments medium brown; capsule medium to dark brown

6. L. parviflora ssp. parviflora

7. Inflorescence fairiy poor in flowers, with long branches and branchlets; bracts and bractlets ciliate to slightly ciliate; perianth segments pale brown to stramineous; capsule blackish brown or pale brown to stramineous

8. Stem with distinctly reddish colour at the

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lowermost internodes; cauline leaves lanceolate, acuminate, green, shiny and thin; perianth segments very acute, scarcely translucent with distinct middle nerve
5. L. parviflora ssp. fastigiata

8. Stem without reddish colour or with indistinct reddish tinge at very base; cauline leaves broadly linear (to lanceolate), acute, bluish to greyish green, dull, thick to thin; perianth segments translucent, middle nerve fairly indistinct; capsule usually blackish brown
6. L. parviflora ssp. melanocarpa


Densely espitose; stem about (10 –) 15 – 25 (– 30) cm tall; leaves pale green, dull, basal leaves 4 – 6 mm wide and up to 20 cm long, cauline leaves 2 – 3, their blades 3 – 5 mm wide; inflorescence about 8 x 10 cm with rigidly divaricate branches and branchlets; bracts and bractlets pale, slightly lacerate and often with a few cilia; perianth segments stramineous to pale brown, often with reddish tinge, equal, long-acuminate with distinct middle nerve and reflexed apex, ca. (1.8 –) 2.0 – 2.2 (– 2.4) mm long; anthers 0.4 – 0.6 (– 0.7) mm long, slightly longer to slightly shorter than filaments; style 0.2 – 0.3 mm long, stigmas 0.7 – 1.5 mm long; capsule slightly exceeding the perianth; valves of capsule ovoid-acute, ca. 1.9 – 2.2 mm long and 1.0 – 1.2 mm wide, broadest close to the middle; seeds brown, 1.0 – 1.3 mm long. Length of stomata of cauline leaves ca. 38 µm (8 – 4 µm; 345 stomata measured on 10 specimens); size of epidermal cells of lower leaf surface ca. 50 – 75 (– 100) x 20 – 25 µm (Fig. 7). Chromosome number apparently not counted.

L. divaricata occurs chiefly in orohemiarctic (upper Hudsonian) woods and lower oorarctic barrens close to the timberline (concerning the zone terminology see e.g. Hämét-Ahti 1965b). Specimens have been seen only from California and Nevada (Fig. 1). It has also been reported from Oregon and Washington (e.g. Piper 1906, Peck 1961, Hitchcock et al. 1969); however, these reports are questionable. For instance, one of the specimens mentioned by Hitchcock et al. (1969; Thompson 2734, WTU) is L. parviflora ssp. fastigiata. I have not seen the other specimens mentioned in floras, but, during visits to several large North American herbaria in 1967, I was not able to find any specimens of L. divaricata collected outside California and westernmost Nevada, and it is obviously endemic to Sierra Nevada. The wide range reported for this taxon in several floras evidently relates to

No distinct hybrids between *L. divaricata* and other *Luzula* species have been met; however, there is one strange specimen (California. Fresno Co., Quibell 4250; UC), which is unusually tall (50 cm) and has poor pollen, deformed capsules and abortive empty seeds. No fungal infection was noted. The reason for this peculiarity is not known, but it is probably not a hybrid.

**Specimens examined**

U.S.A. California. Alpine Co.: Yates 6205 (UC), Gifford 757 (UC), Howden 76 (UC), Graham 4468 (UC). Butte Co.: 1931 Copeland (H), 1939 Copeland (UC), 1932 Copeland (CAN), El Dorado Co.: Robbino 1893 (UC), Grant & Grant 7861 (UC). Fresno Co.: Quibell & Quibell 1543 (WTU), Krueckberg 3476 (WTU), Baegeletti 6588 (UC), Sharsmith 3239 (CAN, UC), Howell 24938 (S), Quibell 7714, 5693 (UC), Irwin 937 (UC), Inyo Co.: 1937 Peirson (UC), Alexander & Kellogg 3403 (UC), 3280 (UC, WTU). Madera Co.: Hanks 349 (UC), Madera-Mono Co.: Sharsmith 2991 (UC), Marinposa Co.: Thomas 493 (UC), Christensen 2075 (UC), Schreiner 1956 (UC). Mono Co.: Clausen 1623 (UC), Munz 19060 (WTU), Howell 14443 (UC), Nevada Co.: Heller 7139 S, UC. Placer Co.: 1892 Carpenter (UC), Shaasta Co.: Gillett 984 (MSC, UC). Tulare Co.: Ferris & Lorraine 10897 (UC, WTU), Howell 17446 (UC), Sharsmith 3821 (UC), Hall & Badevoff 5460 (UC). Tuolumne Co.: Augustine 508 (UC), 1934 Bartholomew (UC), Bolt 435 (UC), Hoover 4173 (UC), Sharsmith 33, 38, 2624 (UC). Co. unknown: Howell 13510 (UC, WTU), Hall 11832 (UC), Brewer 1794 (UC), 1870 Kellogg (CAN), Purpus 3248 (UC), 1873 Lemmon (GIII), 1947 Westergärd (G), 1874 Herb. Lemmon (UC). – Nevada. Washoe Co.: 1905 Kennedy (UC).

2. **Luzula gigantea** Desvaux, J. Bot. 1: 145. 1808

Type: Colombia. In montibus humidis Quinio in regno Santa-fe di Bogotâ, Borbland (not seen).


3. **Luzula hitchcockii** Hámet-Ahti, n. sp.


Etymology: The name is given in honour of Dr. C. L. Hitchcock, the senior author of the vascular plant flora of the Pacific Northwest.

Stolonifera; cauluses (20 – 25) 30 cm alti, foliis 6 – 8 ( – 10) mm latis; inflorescentia anthesiata, ramis erectis vel divaricatis; phylla paulli ciliata; flores castanei vel nigri, 2.5 – 3.5 mm longi; antherae lineares, 1.2 – 1.5 mm longae, filamenti 0.4 – 0.6 mm longis; fructus ovatus, niger vel castaneus, longe mucronatus.

Strongly stoloniferous; stem (20 – 25) 30 cm tall; leaves bright green, fairly thin; basal leaves ca. 5 – 6 mm wide; cauline leaves 3 – 4, being 6 – 8 ( – 10) mm wide and 2 – 6 cm long; in-
florescence ca. 8 × 6 cm, loose, nodding to rather erect, branches often somewhat divaricate; bracts and bractlets usually brown, lacerate to fairly short-ciliate; perianth deep blackish brown to medium brown; perianth segments equal, lanceolate, acute, ca. (2.5 –) 2.7 – 3.0 (– 3.5) mm long; anthers (1.0 –) 1.2 – 1.5 (– 1.6) mm long; filaments 0.4 – 0.6 mm long; style 1 (– 2) mm long, stigmas 1.5 – 2.5 mm long; capsule exceeding the perianth; valves of capsule usually blackish purple-brown, distinctly ovate, (2.8 –) 3.0 – 3.5 (– 3.8) mm long and 1.8 – 2.0 mm wide near the base; beak 1 mm or longer; seeds 1.5 – 1.8 mm long, dark brown. Length of stomata of cauline leaves 46 μm (s ~ 4 μm; 267 stomata measured on 10 specimens); size of epidermal cells of lower leaf surface ca. (75 – 100 – 150 (~ 175)) × 25 – 35 μm (Fig. 7). Chromosome number apparently not counted.

This taxon has been called *L. glabratula* by

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   - *Juncus glabratulus* Hoppe, Herbarium plantarum rariorum praesertim alpinarum, cent. 3 (exs.: unnumbered specimen with printed label). 1808.
   - Type: Salzburg, in monte Untersberg, leg. Hoppe (MW; lectotype, selected here).
the American authors, and it really resembles that European taxon. For instance, they both have well-developed stolons, wide, short and thin cauline leaves, a more or less divaricate inflorescence, a large blackish brown perianth, long anthers, and an ovate capsule with a very distinct beak. The form of the epidermal cells is also fairly similar (Fig. 7). However, they clearly differ from each other in other characters (Table 1, Fig. 3), especially in the stamens: in *L. hitchcockii* the anthers are about 2–3 times as long as the filaments, while in *L. glabrata* they are often up to 8–10 times as long. There are other distinct differences in the size of the perianths and capsules, as shown in Table 1. The colour of the perianth and capsule is also often darker in *L. hitchcockii* than in *L. glabrata*. An anatomical dissimilarity was detected, too: the epidermal cells of the cauline leaves are larger in *L. hitchcockii* than in *L. glabrata* (Fig. 7), and the stomata of the former species also seem to be longer than in the latter (Table 1, Figs. 3, 7). The chromosome number of *L. glabrata* is 2n = 12 (Nordenskiöld 1951); it has apparently not been counted for *L. hitchcockii*. These two taxa are fairly closely related, but it seems to be reasonable to keep them both as species.

*L. hitchcockii* occurs in the upper boreal to oromoecriatic zones from southern British Columbia to Oregon and Montana (Fig. 1). *L. 'glabrata'* has also been reported from Wyoming and southwestern Alberta (e.g. Moss 1959, Daubenmire & Daubenmire 1968, Hitchcock et al. 1969). The record of *L. 'glabrata'* from California (Trinity Co.: Upper Canyon Creek, above Dedrick) by Munz & Keck (1959: 1412) seems to be doubtful and may relate to *L. piperti*, which species has been collected in the same locality (Hitchcock & Martin 5419; UC). *L. hitchcockii* is evidently a slightly oceanic species, which survived the glaciation south of the ice sheet and has not been able to extend its range very much. It seems to favour mesic to fairly dry *Abies lasiocarpa* and *Tsuga mertensiana* woods near the timberline; descriptions of sample plots from this kind of woods have been published, for instance, by Daubenmire & Daubenmire (1968: 98, 101) from southwestern Alberta, eastern Washington and northern Idaho.

The ecology of the European *L. glabrata* seems to be similar to that of its American relative: it occurs in the upper oroboreal to oromoecriatic zones in the eastern Alps (cf. Braun-Blanquet & Braun-Blanquet 1931, Hess et al. 1967, Oberrdorfer 1970). In Europe, there is also another taxon, *L. desvauxii* Kunth, which is fairly close to *L. glabrata* and which was earlier regarded as a variety of that species, e.g. by Buchenau [1906: *L. glabrata* var. *desvauxii* (Kunth) Buch.]. However, nowadays *L. desvauxii* is usually considered a distinct species (cf. Kunz 1960, Ehrendorfer 1970, Hess et al. 1967), apparently with good justification. For instance, *L. desvauxii* has narrower and longer cauline leaves, a looser and more nodding panicle, a shorter perianth, shorter anthers and smaller seeds than *L. glabrata*. Its chromosome number is 2n = 12 (Lambert & Giesi 1967), the same as in *L. glabrata*.
L. hitchcockii is a very distinct and invariable taxon and is not usually confused with any other Luzula species than L. glabrata. Only specimens strongly infected by Ustilago vuijekii Oud. & Beij. may display some strange features; for instance, such plants have only a few flowers, their branches may be unusually short, their open anthers very wide, etc. (cf. HÄMÉT-AHTI 1972).

No apparent hybrids between L. hitchcockii and other Luzula species have been found among the specimens examined.

Specimens examined


Canada. S British Columbia: 49° 2′ N, 114° 12′ W, Taylor et al. 3413 (UC), 49° 04′ N, 120° 12′ W, Calder et al. 19899 (UC), Manning Park, 1953 Calder & Saville 11642 (DAO, WTU), Scoggan 15802 (CAN), Beamish & Vrugtman 60821 (OULI).

4. Luzula parviflora (Ehrh.) Desv. ssp. parviflora s. lat.

Juncus parviflorus Ehrhart, Beitr. Naturk. 6: 139, 1791.

Loosely cespitose, with or without short stolons; stem about 50–60 cm tall with some reddish color at very base; leaves dull, thick, yellowish green; basal leaves 12–17 cm long and 5–8 mm wide; cauline leaves 3–5, lanceolate, acuminate, 3–8 mm wide and up to 7–9 cm long; inflorescence fairly rich in flowers with long nodding major branches but short (often very short) ultimate branches; bractlets and bractlets almost entire to slightly lacerate, medium brown; perianth medium to dark brown; perianth segments fairly broad, lanceolate, acute and crenate at the apex, not rigid, 2–2.5 mm long; anthers 0.4–0.5 mm long, about equal to filaments, stamens about 1 mm long; capsule dark brown, elliptical to rounded and sometimes slightly notched at apex, with short beak (0.3 mm), hardly exceeding the perianth; valves of capsule 1.8–2.3 mm long and 0.8–1.0 mm wide; seeds 1.1–1.3 mm long, brown, with some fibrils at the micropylar end. Length of stamena of cauline leaves 38 μm (30–33 μm) measured on 10 specimens; size of epidermal cells of lower surface ca. 75–100 × 20–30 μm (Fig. 7). Chromosome counts evidently made on this subspecies have given the numbers 2n = 24 (LÖVE & LÖVE 1961, PACKER 1964, HEDBERG 1967, KNABEN & ENGELSKJÖN 1967, ZHUROVA 1967, KNABEN 1968, LÖVE 1968) and 2n = 22 (HÄMÉT-AHTI & VIRHANKOSKI 1971). 2n = 36 reported in MOORE (1970) is an error.

In North America L. parviflora ssp. parviflora s. lat., which is slightly oceanic, occurs in the upper oroboreal (northern boreal) to oro-nemarctic (hemiarctic) zones, from Alaska (excl. most of the Arctic slope) along the mountains to California and Colorado. In Canada its eastern limit is unknown. Most of the Greenland specimens also seem to be referable to this subspecies rather than to the eastern North American ssp. melanocarpa. The descriptions of L. parviflora in southwestern North American floras do not fit this race but ssp. fastigiala; exceptions are the floras concerning the area of the southern Rocky Mts. (e.g. WEBER 1967).

Ssp. parviflora occurs in moist rich forests, woods and thickets, on river sides, along brooks, in seepage and herb meadows, and around springs, preferring sites fairly rich in nutrients.

L. parviflora ssp. parviflora s. lat. is closest to HULTÉN’s (1937: 87–89, 1958) circumpolar arctic-montane species; however, its range is not completely circumpolar, having gaps (cf. e.g. the maps in HULTÉN 1962, 1968b, TOLMACHEV 1963). Detailed studies will probably lead to its division into further taxa; for instance, the Scandinavian population is somewhat dissimilar to the North American ones.
Usilago vuieckii has been found on some specimens of L. parviflora ssp. parviflora collected from Yukon and Alaska (cf. Hämät-Ahti 1972).

5. Luzula parviflora ssp. fastigiata (E. Meyer)

Hämät-Ahti n. comb.


Stolons short; stem about 30 – 50 (– 70) cm tall, lowermost internodes with distinct reddish colour; leaves bright green, thin and shiny, basal leaves up to 8 mm wide and 10 cm long; cauline leaves 4 – 5, lanceolate, acuminate, up to 6 mm wide; inflorescence up to $13 \times 12$ cm but few-flowered, branches much extended, sometimes fairly divaricate; bracts with some to many cilia, bractlets entire to slightly lacerate; perianth pale brown to stramineous; perianth segments lanceolate, acute, with fairly distinct middle nerve, rigid, 1.8 – 2.2 mm long.

Fig. 4. Luzula parviflora ssp. fastigiata (E. Meyer) Hämät-Ahti (Queen Charlotte Is.; Calder & Taylor 35337; H). Photo: Mauri Korhonen.
and 0.5–0.7 mm wide; anthers 0.3–0.4 (–0.4) mm long, usually about half as long as filaments, stamens 1.6–1.7 (–1.7) mm long; capsule pale brown to stramineous, usually clearly exceeding perianth; valves of capsule 2–2.5 mm long and 1–1.2 mm wide, oval, with very short beak (0.2 mm); seeds dark brown, 1.2–1.3 mm long, with some fibrils at micropylar end. Length of stomata of cauline leaves ca. 42 µm (8 μm; 370 stomata measured on 10 specimens); size of epidermal cells of lower leaf surface ca. 125–175 x 20–25 µm (Fig. 7). The only chromosome number evidently counted for this race is 2n = 24, reported by Taylor & Mulligan (1968) from the Queen Charlotte Islands (under the name L. parviflora 'lowland phase').

Haenke's specimen from Nootka is rather poor but it obviously represents this western race, which has been reported as L. parviflora ssp. divaricata (S. Wats.) Hult. by Hultén (1943, 1962, 1968a, 1968b). Though resembling L. divaricata to some extent, it must be included in L. parviflora rather than in L. divaricata. For instance, L. divaricata is lower (usually below 30 cm) with a rigidly divaricate inflorescence, its perianth segments have a long-acuminate, usually reflexed apex and its capsules hardly exceed the perianth.

These two taxa differ from each other also in zonal distribution: L. parviflora ssp. fastigiata occurs in the temperate to boreal zones and L. divaricata in the oro-hemi-arctic to lower oro-arctic zones, close to the timberline. L. divaricata has a small range in the Sierra Nevada, California (Fig. 1); L. parviflora ssp. fastigiata seems to occur in oceanic western North America from the Aleutian Islands to California (Fig. 5). In several western North American floras (e.g. Jepson 1923, Abrams 1940, Munz & Keck 1959) L. parviflora is reported as often having pale-coloured perianths and capsules, and this also indicates that ssp. fastigiata is the commonest race of L. parviflora occurring in the westernmost United States.

The habitats of ssp. fastigiata are in mesic to moist forests. For instance, there are several descriptions of sample plots published by Daubenmire & Daubenmire (1968: 84, 87, 92, 94, 96, etc.) from oroboreal forests (Abies grandis, A. lasiocarpa and Thuja plicata as predominant trees) in northern Idaho, southwestern Alberta and eastern Washington which contain records of 'L. divaricata', 'L. wahlehnbergii' and L. parviflora. According to herbarium specimens collected by R. F. Daubenmire, the two first-mentioned names, at least, evidently often relate to L. parviflora ssp. fastigiata.

L. parviflora ssp. fastigiata obviously hybridizes with ssp. parviflora and the intermediates are not uncommon (Fig. 5). They have more or less ciliate bracts, long branches in the inflorescence, except the ultimate ones, which are usually short, yellow brown to brown perianth segments and brown to dark brown capsules,
Table 2. Comparison of some characters of *L. parviflora* ssp. *parviflora*, ssp. *fastigiata* and ssp. *melanocarpa*.

<table>
<thead>
<tr>
<th>Character</th>
<th>ssp. <em>parviflora</em></th>
<th>ssp. <em>fastigiata</em></th>
<th>ssp. <em>melanocarpa</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Full-grown stem</td>
<td>50 – 60 cm tall, with some reddish colour at very base</td>
<td>30 – 50 cm tall, lowermost internodes with very distinct red colour</td>
<td>50 – 90 cm tall, without reddish colour or with indistinct tinge at very base</td>
</tr>
<tr>
<td>Cauline leaves</td>
<td>yellowish to bluish green, dull, thick, lanceolate, acuminate, up to 8 mm wide</td>
<td>bright green, shiny, thin, lanceolate, acuminate, up to 6 mm wide</td>
<td>bluish to grayish green, dull, broadly lanceolate, acute, up to 10 mm wide</td>
</tr>
<tr>
<td>Inflorescence</td>
<td>many-flowered, branches fairly long, branchlets short</td>
<td>few-flowered, branches long, often arcuate, branchlets long, capillary (Fig. 5)</td>
<td>few-flowered, branches long, arcuate, branchlets long, capillary</td>
</tr>
<tr>
<td>Bracts</td>
<td>entire</td>
<td>entire</td>
<td>entire</td>
</tr>
<tr>
<td>Bracelets</td>
<td>lacerate to indistinctly ciliate</td>
<td>strongly ciliate</td>
<td>slightly ciliate</td>
</tr>
<tr>
<td>Perianth segments</td>
<td>brown to dark brown, not translucent, 2 – 2.5 mm long, broadly lanceolate, often erose at apex, not rigid, with indistinct middle nerve</td>
<td>pale brown to strawmeneous, fairly translucent, 1.8 – 2.5 mm long, lanceolate, acute, rigid, with distinct middle nerve</td>
<td>brown to pale brown, translucent, 1.4 – 2.8 mm long, lanceolate, acute, fairly rigid with fairly indistinct middle nerve</td>
</tr>
<tr>
<td>Anthers</td>
<td>about equal to filaments</td>
<td>distinctly shorter than filaments</td>
<td>about equal to filaments</td>
</tr>
<tr>
<td>Capsule</td>
<td>dark brown, hardly exceeding the perianth</td>
<td>pale brown to strawmeneous, distinctly exceeding the perianth</td>
<td>dark brown, distinctly exceeding the perianth</td>
</tr>
<tr>
<td>Epidermal cells of lower leaf surface</td>
<td>ca. 75 – 100 x 20 – 30 μm (Fig. 7)</td>
<td>ca. 125 – 175 x 20 – 25 μm (Fig. 7)</td>
<td>ca. 60 – 100 (– 120) x 20 – 25 (– 30) μm (Fig. 7)</td>
</tr>
<tr>
<td>Zonal distribution</td>
<td>upper oroboreal (northern boreal) to oroziemiatic (hemiarctic)</td>
<td>temperate to (oro)boréal</td>
<td>boreal to hemiarctic</td>
</tr>
</tbody>
</table>

etc. Especially the ciliate bracts have led many authors to determine these intermediates as *L. wahlenbergii* (cf. Hultén 1962: 63). The common occurrence of *L. parviflora* ssp. *parviflora* ≥ ssp. *fastigiata* makes *L. parviflora* s. lat. very variable in western North America, excluding most parts of Alaska and the Yukon, where ssp. *parviflora* s. lat. is the only race.

*L. parviflora* ssp. *fastigiata* clearly belongs to the group of oceanic plants which during the maximum glaciation apparently survived in southern Beringia and also south of the glaciated region, the two populations joining up again fairly early (cf. Hultén 1937: 66). More intensive study might possibly reveal some differences between the northern and southern populations.

No smut-infected specimens of this race have been seen during this study.

**Specimens of *L. parviflora* ssp. *fastigiata* examined**

*U.S.A.* Alaska, Aleutian Is.: Amchitka L., Reich & McCann 390, 621 (OUL). Central Pacific Coast Dist.: 1922 Stejneger (S), 1937, 1938 and 1940 Norberg (S), Eyerdam 5932 (S), Calder 6018 (UC), 1961 Fay (S), Eastern Pacific Coast Dist.: Barclay (S), 1868 Tiling (H), 1897 Evans (S), 1895 Howell (S), Coville & Kearney 816 (S), Walker 643 (S), Heller 14908 (UC), Anderson 22439 (S), Hultén 8174, 8176, 8404, 8545 (S), Eyerdam 3007, 5403 (S), Purser 7595 (S), Neiland 106, 641 (S). – Washington. King Co.: Otis 778 (UC), Okanogan Co.: Sandberg & Leiberg 685 (S), Snohomish Co.: 1928 Grant (H), Co. unknown, 1902 Blasdale (UC), 1859 Lyall (S), – Oregon. Lincoln Co.: Constance & Beetle 2642 (S), Multnomah Co.: Thompson 2734 (WUT), Washington Co.: 1931 Wall (S), – Idaho. Boise Co.: Hitchcock & Millhick 9995 (UC), Bonner Co.: Daubenmire 43344 (UC), Clear- water Co.: Shursmith 3581 (S), Kootenay Co.: 1891 Sandberg (S), Latah Co.: Dillon 564 (S), Co. unknown, Epling & Honcke 9374 (S), – California. Humboldt Co.: Balls 10272 (S), Tracy 7171 (UC), Madera Co.: Hanks 349 (UC), Tuolumne Co.: Bolt 435 (UC), – Utah. Uintah Co.: 1911 Clemens (UC), Co. unknown, La Sal, 1899 Purpos (UC), – Colorado. Larimer Co.: Clokey 3742 (S), Co. unknown, Keehr Pass, Tidstrom 3897 (S),

Specimens of *L. parviflora* ssp. *parviflora* ≡ ssp. *fastigida* examined


6. **Luzula parviflora** ssp. *melanocarpa* (Michx.) Hämét-Ahti, n. comb.


Concerning other nomenclatural combinations, see Buchanan (1906: 62) and Hitchcock et al. (1909: 217).

Cespitose with short stolons; stem about 60–90 cm tall, usually without reddish colour or with indistinct reddish tinge at the very base; leaves dull, bluish green; basal leaves up to 20 cm long and 8–10 mm wide; cauline leaves 4–6, broadly lanceolate to linear, acute, 8–12 cm long and (6–) 8–10 mm wide; inflorescence large, about 12 (–20) × 8 cm, poor in flowers, with very long branches and long, loosely spreading to reflexed branchlets; bracts with a few cilia, bractlets entire to very slightly lacerate; perianth brown to pale brown, often translucent; perianth segments 1.8–2.5 mm long and 0.5–0.7 mm wide, acute, rigid; stamens 0.8–1.2 mm long, anthers slightly shorter to slightly longer than filaments; capsule dark brown (sometimes pale brown), distinctly exceeding perianth, 0.8 mm long; valves of capsule 1.8–2.2 mm long and 1.4–1.6 mm wide, oval; seeds 1.2–1.4 mm long, dark brown with some fibrils at micropylar end. Length of stomata of cauline leaves ca. 40 μm (s=4 μm; 424 stomata measured on 10 specimens); size of epidermal cells of lower surface ca. 60–100 (–120) × 20–25 μm (Fig. 7). Chromosome number 2n = 24 (Löve & Löve 1966).

Concerning its separation from the other races of *L. parviflora*, see Table 2.

*L. parviflora* ssp. *melanocarpa* occurs in eastern North America, chiefly from southern boreal to (oro)hemiarctic zone, and its range extends from Labrador and Newfoundland to Saskatchewan and Minnesota in the west and along the mountains to New York State in the south, at least. This race has also been reported from Europe (e.g. Hultén 1962), western North America (Hultén 1968b) and eastern Siberia (Tolmachev 1963) but these records obviously relate to specimens of ssp. *parviflora* with dark-coloured capsules and pale perianths. Such plants represent occasional colour variants of ssp. *parviflora* s. lat. rather than ssp. *melanocarpa*. It seems certain that most of the eastern North American specimens of *L. parviflora* (excl. those from Greenland) belong to ssp. *melanocarpa*, although they sometimes may have fairly pale capsules.

No hybrids or stunt-infected specimens of this race have been observed during this study.

7. **Luzula piperi** (Gov.) M. E. Jones


Cespitose, stem 20–30 (–35) cm tall, without reddish colour; leaves thick, firm, dull, bluish green; basal leaves 5–10 cm long and 3–4 mm wide; cauline leaves 3, linear, up to 3–7 cm long and 3–5 mm wide; inflorescence nodding, about 5 × 3 cm, rich in flowers; bracts and bractlets brown and strongly ciliate with long, curly cilia; perianth dark brown; perianth segments (1.6–) 2–2.3 (–2.5) mm long, acute; anthers (0.4–) 0.4–0.4 (–0.8) mm long, slightly longer to slightly shorter than filaments, the whole length of stamens being 0.8–1.2 mm; style 0.2–0.4 mm, stigmas about 1 mm long; capsule exceeding perianth; valves of capsule 1.8–2.2 (–2.5) mm long and 1–1.4 mm wide, elliptical; seeds light yellowish brown, 1–1.2 (–1.4) mm long with a few fibrils at micropylar end. Length of stomata of cauline leaves 36 μm (s=3 μm; 291
L. piperi occurs in the oceanic oroarctic (evidently lower oroarctic) zones from California through the coastal part of Alaska, the Aleutian Islands and southern Kamchatka to the northern Kuril Islands (Fig. 6). It seems to prefer snowbeds and mesic oroarctic heaths but it has also been collected on thin peat and rocky soils. It is a northern Pacific, oceanic species, which very clearly belongs to Hultén's (1937) western American plants reaching the Bering Sea, radiating from coastal refugia.

Hitchcock (in Hitchcock et al. 1968) considered that specimens of this species in herbaria partly belong to L. glabrata and partly to L. parviflora and regarded the type specimen of L. piperi as a dark-coloured specimen of L. parviflora. After studying L. piperi in the field in Alaska and in many large North American herbaria (1967) and after checking the type specimen, I cannot agree with Hitchcock's opinion. L. piperi is a distinct taxon, which differs clearly from the variable L. parviflora in its linear, thick, dull cauline leaves, strongly curly-ciliate bracts and bractlets, and yellow seeds. L. glabrata differs from L. piperi in its long stolons, wide, short and thin cauline leaves, longer perianth segments, long anthers, ovate, long-beaked capsule, etc. In addition, the zonal distribution of these three taxa is different: L. piperi is a distinctly oroarctic plant, whereas L. glabrata seems to occur in the upper oroboreal to oroalpine zones and L. parviflora s. lat. has in western North America a very wide zonal range from the temperate to oroalpine zones.

The type specimen of L. piperi was collected very late in the autumn and its perianth segments, bracts and bractlets are somewhat eroded, as is usual in wood rushes, but it undoubtedly represents L. piperi and not L. parviflora.

Hultén (1968a, 1968b) regards L. piperi as a subspecies of L. wahlenbergii and reports the occurrence of some intermediate forms; however, I cannot agree with Hultén regarding the intermediate forms, and the differences between the two taxa appear to be so great that it seems better to regard them as distinct species. There is also no reason to treat L. piperi as a race of L. parviflora; for instance, though these two taxa sometimes grow together, only one specimen has been found which is obviously a hybrid (Montana: Ravalli Co., Hitchcock & Muhlick 15340; UC). This specimen has empty anthers and deformed capsules with small empty seeds and its appearance is intermediate between L. parviflora and L. piperi.

Ustilago pyjekii has been found on some specimens of L. piperi collected from Washington, British Columbia, and Alaska (cf. Hämet-Ahti 1972).
Specimens examined


The map also includes the specimens listed in Hämäläinen 1965a: 18–19.

8. Luzula wahlenbergii Ruprecht, Fl. Samojed.

Cisural. 58. 1845

Concerning synonyms and other nomenclatural combinations, see Buchanan (1906: 63).

Densely cespitose; stem 22–30 cm tall, often with reddish colour at base; leaves green, shiny and thin; basal leaves 5–10 cm long and 3–5 mm wide; cauline leaves (1–2), lanceolate, up to 3.5 cm long and 2–4 mm wide; inflorescence partly nodding, rather poor in flowers, about 4 x 3 cm; bracts and bracteoles strongly ciliate with curly cilia, brown; perianth brown; perianth segments 2–2.5 mm long, acute, anthers 0.4–0.5 mm long, slightly longer to slightly shorter than filaments, length of stamen being 0.7–1.0 mm; style less than 0.5 mm, stigmas ca. 1 mm long, capsule brown, slightly exceeding perianth; valves of capsule 2–2.5 mm long and 1.1–1.5 mm wide, broadly elliptical; seeds dark reddish brown with many slender fibrils at micropylar end, 1.2–1.4 mm long. Length of stoma of cauline leaves ca. 42 μm (s ~ 6 μm; 218 stomata measured on 10 specimens); size of epidermal cells of lower surface ca. 75–100 (~ 150) x 25–35 μm (Fig. 7). The chromosome number 2n = 24 is reported from Europe, eastern Siberia, Alaska, and Arctic Canada (Knaебен & Engelskjøn 1967 and the papers cited in it; Hedberg 1967, Knaебен 1968, Zhukova 1967); the number 2n + 36 mentioned, e.g., by Hitchcock et al. (1969) and Bolkhovskikh et al. (1969) is evidently the result of an incorrect determination of the voucher specimen (cf. Nordenskiöld 1951: 329).

L. wahlenbergii is a low arctic (lower oroarctic) circumpolar species; in North America it occurs in Greenland (Holmen & Mathisen 1953), Arctic Canada (Porsild 1957) and northern Alaska (cf. maps in Hämäläinen 1965a, Hultén 1968b). Its habitats seem to be moist, acid sites on thin peat or rocky soil.

The characters distinguishing L. wahlenbergii most clearly from L. parviflora s. lat. are its fairly low stem, the number of cauline leaves (1–2), and the bracts, which have long, curly cilia; those distinguishing it from L. piperi are the shiny, thin leaves, lanceolate cauline leaves, and dark reddish brown seeds (cf. also the detailed table in Hämäläinen 1965a).

The literature records of the occurrence of L. wahlenbergii in western Canada and the U.S.A. (outside the Arctic) generally refer to L. piperi or L. parviflora. In the nine large North American herbaria visited I was not able to find any specimen of L. wahlenbergii collected outside Arctic Canada or northern Alaska; all the plants under this name represent L. piperi or L. parviflora. Also the specimens mentioned by Hrrncrook et al. (1969: 219) under L. wahlenbergii from Oregon and Washington (including those in the figure on page 218) belong to L. piperi.

No hybrids between L. wahlenbergii and other species of Luzula and no specimens infected by smut were found during this study.

Species excluded

Luzula subcongesta (S. Wats.) Jepson has sometimes been included in L. parviflora as a variety (cf. Watson 1880: 202, Buchanan 1890, 1906). After checking a specimen of the authentic material determined by S. Watson (U.S.A. California: Mt. Shasta, 1860–62 Brewer 1378; GH, UC), I am inclined to include it in the subgenus Luzula rather than in the subgenus Anthelia. L. subcongesta may be related to the northern group containing L. arctica, L. arcuata, L. confusa and L. kiejmaniana. According to
Nordenskiöld (1951) the chromosome number of _L. subcongesta_ is 2n = 24 and the chromosome pattern is very similar to those of _L. parviflora_ and _L. wahlenbergii_, consisting of chromosomes of the «BL»-type; however, the same kind of chromosome pattern is also found in the other subgenera of _Luzula_ (cf. Nordenskiöld 1951).

This taxon, which occurs in the Sierra Nevada (e.g. Jepson 1923, Abrams 1940, Munz & Keck 1959, Peck 1961), is accordingly left out of this study.

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