

8. POLYTRICHACEAE Schwägrichen

Gary L. Smith Merrill

Plants small, medium to large, densely to loosely caespitose or scattered among other bryophytes, rarely with individual plants scattered on a persistent protonema. **Stems** erect, acrocarpous, from a ± developed underground rhizome, simple or rarely branched, bracteate proximally, grading gradually or abruptly to mature leaves. **Leaves** various, with a chartaceous, sheathing base and a divergent, firm-textured blade (polytrichoid), or the whole leaf membranous and sheath not or weakly differentiated, the blade rarely transversely undulate, crisped and contorted when dry; adaxial surface of blade with numerous closely packed longitudinal photosynthetic lamellae across most of the blade, the marginal lamina narrow, or the lamellae restricted to the costa, flanked by a broad, 1 (rarely 2)-stratose lamina, rarely with abaxial lamellae; margins 1(–3)-stratose, entire, denticulate, serrate, or toothed (in *Atrichum* bordered by linear, thick-walled cells); costa narrow in basal portion, in the blade abruptly broadened and diffuse, smooth or toothed adaxially, rarely with abaxial lamellae, in cross section with a prominent arc of large diameter guide cells and an abaxial stereid band; lamellae entire, finely serrulate, crenulate, or coarsely serrate, the free margin smooth or cuticular-papillose, the marginal cells in cross-section undifferentiated or sharply distinct in size and/or shape from those beneath; transition in areolation from sheath to blade gradual or abrupt, with “hinge-tissue” at the shoulders (except *Atrichum* and *Psilopilum*); cells of back of costa (or cells of the membranous lamina) typically in longitudinal rows, ± isodiametric to transversely elongate-hexagonal. **Vegetative reproduction** none, or by proliferation of an underground rhizome. **Sexual condition** dioicous or rarely monoicous; male inflorescence indeterminate, innovating from the center and continuing the growth of the stem, often several successive perigonia per shoot; female inflorescence terminal, perichaetial leaves long-sheathing or not much differentiated. **Seta** solitary or rarely several from the same perichaetium. **Capsule** obtusely to sharply (2–)4(–6)-angled, with indistinct longitudinal angles or ridges, or terete; hypophysis tapering and indistinct or delimited by a constriction at base of capsule; exothecium smooth, mammillose, or scabrous; stomata present (absent in *Atrichum* and *Pogonatum*); peristome pale or strongly pigmented, nematodontous, with a single series of [16–]32–64 rigid, unjointed teeth composed of elongate, fiber-like, sinuate cells, the teeth simple or compound, attached by their tips to the epiphragm (tympanum) covering the capsule mouth. **Calyptra** cucullate, with a matted felt of hairs arising from its tip and

covering all or part of the capsule, or the calyptra sparsely ciliate to smooth. **Spores** minute and echinulate, or larger and finely papillose.

Genera 22, species ca. 260 (9 genera, 38 species in the flora): nearly worldwide.

The Polytrichaceae are widely distributed in all climatic zones except the lowland tropics and include many large, common, and familiar North American mosses. These “hair-cap mosses” have no close living relatives, and have a long (but disjunctive) fossil record (*Eopolytrichum*) from the Late Cretaceous of Georgia, United States (A. S. Konopka et al. 1997). The family is remarkable for the structural complexity of both gametophyte and sporophyte found in many of its members. The stems of robust taxa (*Polytrichum*) have a conspicuous central strand composed of hydrome and leptome, and traces extending into the leaves; in other genera the central strand is weak and indistinct.

The following descriptions use the shorthand term “polytrichoid” for taxa with a growth form and leaves like those of *Polytrichum*. The best analogy to the polytrichoid leaf is the grass leaf, with a clear distinction between a sheathing base and divergent blade. Typically a wedge-shaped group of transversely elongate, incrassate cells (“hinge tissue”) is present at the shoulders or just above. Most polytrichoid taxa have a hyaline-margined sheath, with a sharply defined border of thin-walled, decolorate cells. The leaves of *Atrichum* have a slender costa and a broad, membranous lamina. In *Bartramiopsis* and *Lyellia*, however, the lamellae are restricted to the “costa” and the broad “lamina” is 2-stratose. In the polytrichoid leaf the distinction between costa and lamina becomes blurred. The conducting strands are confined to a median band, flanked by an ambiguous zone bearing closely packed lamellae but only a few cells in thickness, and a narrow, usually 1-stratose marginal lamina. Gary L. Smith (1971) suggested that lamellae originally covered the adaxial surface of the leaf, and the broad membranous lamina developed as conducting strands and lamellae were restricted to the median portion.

As demonstrated by S. O. Lindberg (1868) the form of the marginal cells of the lamellae is often sufficient to distinguish between species of Polytrichaceae. Free-hand sections with a razor blade are adequate in most cases. Sections should be made from ordinary vegetative leaves, in the middle $\frac{1}{3}$ (or in polytrichoid leaves, midway between the tip and the base of the blade). Lengths of lamellae should also be scraped from the leaves to be viewed in profile. Median cells of the lamina are best measured individually. The leaf cells are typically aligned in \pm regular longitudinal rows, but it is difficult to measure a group of cells and divide to obtain an average cell width since the cells are not aligned transversely.

The peristome teeth are unique among mosses in being composed of compact bundles of whole, fiber-like cells. The teeth are not composed of remnants of wall thickenings as in arthrodontous mosses, but form by intrusive growth and elongation of living cells. Accordingly, the peristomes are not homologous. The teeth may be simple (with a single median line), or compound (the outlines of two teeth visible on the outer face of each tooth), although the exact nature of this difference is not well understood. The sinus between these “teeth” may be broad (*Oligotrichum*), or narrow and obscured (*Pogonatum*). The height of the peristome is measured from the tips of the teeth to the capsule rim, seen from without. The term “basal membrane” is not used. The generic classification used in this treatment follows that of Gary L. Smith (1971) with few modifications.

SELECTED REFERENCES Frye, T. C. 1910. The Polytrichaceae of western North America. Proc. Wash. Acad. Sci. 12: 275–281. Long, D. G. 1985. Polytrichaceae. In: G. S. Mogensen, ed. Illustrated moss flora of arctic North America and Greenland. 1. Meddel. Grønland, Biosci. 17: 9–57. Smith, Gary L. 1971. A conspectus of the genera of Polytrichaceae. Mem. New York Bot. Gard. 21(3): 1–83.

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1. Protonema persistent; individual leafy plants small and scattered 7. *Pogonatum* (in part), p. 155
 1. Protonema ephemeral; leafy plants gregarious, loosely tufted or caespitose.
 2. Lamellae 10 or fewer and confined to median portion of blade, often loosely spreading and wavy.
 3. Lamina 2-stratose, \pm firm, the upper layer of laminar cells strongly mammillose.
 4. Margins of sheath entire; lamellae entire; leaf tip with a slender, caducous hair; plants polytrichoid 8. *Lyellia*, p. 159
 4. Margins of sheath ciliate; lamellae coarsely serrate; leaf tip not ciliate; plants slender and wire-like 9. *Bartramiopsis*, p. 161
 3. Lamina 1-stratose, broad and membranous, the cells not mammillose above (or if mammillose, then the leaf bordered by thick-walled elongate cells).
 5. Leaf margins bordered by narrow, thick-walled cells, sharply toothed; lamina often transversely undulate, the back of lamina with diagonal rows of teeth; abaxial lamellae absent 6. *Atrichum*, p. 147
 5. Leaf margins serrulate to entire, not bordered by narrow, thick-walled cells; lamina not undulate and not toothed on back; abaxial lamellae often present.
 6. Leaves not hyaline-margined; well-developed abaxial lamellae often present on both costa and lamina 4. *Oligotrichum*, p. 142
 6. Leaves narrowly bordered in part by thin-walled, hyaline cells; abaxial lamellae absent or restricted to costa near leaf apex 5. *Psilopilum*, p. 145
 2. Lamellae 20 or more, occupying most of the leaf width, compact and straight.
 7. Margins of lamellae papillose (or appearing so in cross-section).
 8. Leaf sheath not hyaline-margined; marginal cells of lamellae rectangular and flat-topped 7. *Pogonatum* (in part), p. 155
 8. Leaf sheath hyaline-margined; marginal cells of lamellae rounded to elliptic to pyriform.
 9. Marginal cells in profile irregularly striolate and pitted 3. *Meiotrichum*, p. 141
 9. Marginal cells in profile distinctly papillose, with rounded papillae.
 10. Marginal cells pyriform, lateral walls strongly thickened, lumen narrowly pentagonal 1. *Polytrichastrum* (in part), p. 124
 10. Marginal cells elliptic, thick-walled, the distal wall broadly convex 7. *Pogonatum* (in part), p. 155
 7. Margins of lamellae smooth.
 11. Marginal lamina greatly expanded and sharply inflexed, entire, overlapping and enclosing the lamellae, the cells transversely elongate 2. *Polytrichum* (in part), p. 133
 11. Marginal lamina narrow, serrate or toothed (if subentire then not broadly inflexed, the cells \pm isodiametric).
 12. Lamellae \pm entire in profile, the apical cells rounded in cross-section, only slightly taller than those beneath, or transversely ovate.
 13. Leaves with a distinct sheathing base and a firm, divergent blade, the sheath entire, hyaline-margined 1. *Polytrichastrum* (in part), p. 124
 13. Leaves lax, only weakly differentiated into sheath and blade, toothed nearly to the base, not hyaline-margined 7. *Pogonatum* (in part), p. 155
 12. Lamellae crenulate in profile, the apical cells differentiated, retuse or flat-topped in cross-section.
 14. Costa rounded in cross-section, forming a low ridge on back of blade, the arc of guide cells narrow (8–12 cells wide); median sheath cells short-rectangular (to 5:1) to rhomboidal 1. *Polytrichastrum* (in part), p. 124
 14. Costa in cross-section broad and flat, the arc of guide cells 18–24 cells wide; median sheath cells linear (as 20:1) 2. *Polytrichum* (in part), p. 133

Alternative Key

1. Calyptra densely hairy.
 2. Capsules without stomata, terete or with 6–8 longitudinal ridges; peristome colored; exothecium scabrous 7. *Pogonatum*, p. 155
 2. Capsules with stomata, angled or cylindrical; peristome teeth pale; exothecium smooth or mammillose.
 3. Urn rather bluntly 4(–6)-angled or terete; exothecium smooth, the exothecial cells without pits or with a diffuse thin-spot; peristome teeth not keeled 1. *Polytrichastrum*, p. 124
 3. Urn sharply alate, especially with age; exothecium mammillose, the exothecial cells bulging, with a sharply-defined pit; teeth with a thin vertical keel on the inner face 2. *Polytrichum*, p. 133
1. Calyptra sparsely hairy or smooth.
 4. Lamellae numerous, occupying most of the leaf width; capsule bilaterally compressed, 4-angled, the two uppermost angles often more prominent, forming a crest 3. *Meiотrichum*, p. 141
 4. Lamellae 10 or fewer, confined to the median portion of leaf; capsule 2-angled or terete.
 5. Leaf lamina 2-stratose; peristome none.
 6. Lamellae entire; leaf sheath entire; leaf tip with a caducous, uniseriate hair; plants polytrichoid; [capsule sharply 2-angled and lunate in section] 8. *Lyellia*, p. 159
 6. Lamellae coarsely serrate; leaf sheath ciliate; leaf tip not ending in a slender, uniseriate hair; plants slender and wire-like; capsule turbinate 9. *Bartramiopsis*, p. 161
 5. Leaf lamina 1-stratose; peristome present.
 7. Peristome teeth compound (double), with a broad U-shaped sinus on the outer face of each tooth; lamina and costa often with abaxial lamellae 4. *Oligotrichum*, p. 142
 7. Peristome teeth simple, without a U-shaped sinus; lamina without abaxial lamellae (except on back of costa near apex), the costa often toothed at back.
 8. Capsules with stomata; leaf margins entire, bordered (at least in part) by thin-walled, hyaline cells 5. *Psilopilum*, p. 145
 8. Capsules without stomata; leaf margins toothed and strongly bordered by thick-walled, linear cells 6. *Atrichum*, p. 147

1. POLYTRICHASTRUM G. L. Smith, Mem. New York Bot. Gard. 21(3): 35. 1971
 - [Genus *Polytrichum* and Latin *-astrum*, incomplete resemblance]

Gary L. Smith Merrill

Plants polytrichoid, medium-sized to robust, in loose tufts. **Stems** simple to sparingly (or fasciculately) branched, arising from a short underground rhizome. **Leaves** with ± differentiated sheathing base and divergent blade; sheath entire, hyaline-margined, often nitid, ± abruptly contracted to the blade, the shoulders with well-developed hinge tissue; marginal lamina sharply toothed to entire; costa typically short-excurrent or (in perichaetial leaves) prolonged into a toothed awn, rarely the apex cucullate; lamellae numerous, closely spaced, occupying most of the distal surface of the blade, the margins ± entire, finely serrulate or crenulate in profile, smooth or coarsely papillose, the marginal cells in section undifferentiated or sharply distinct. **Sexual condition** dioicous or polygamous. **Seta** solitary. **Capsule** terete or more commonly 4–6-angled, the hypophysis tapering or distinct and cylindric but not sharply delimited; exothecium smooth, the cells not bulging or papillose, not pitted, sometimes with a diffuse thin spot on the outer wall; stomata numerous; operculum rostrate with a distinct beak; peristome not deeply pigmented, the teeth regularly 64, or somewhat fewer and irregular with some teeth compound, not keeled at back; epiphragm with erect tooth-like processes opposite the peristome teeth and loosely attached to their inner face. **Calyptra** cucullate, hidden by an interwoven mat of hairs covering the distal portion of capsule. **Spores** finely papillose.

Species ca. 20 (8 in the flora): widespread in temperate and boreal latitudes in Northern Hemisphere; scattered in the Southern Hemisphere.

Species of *Polytrichastrum* have a peristome of the *leiodont* type (S. O. Lindberg 1868). The capsule is terete or obtusely (in fresh capsules) 4–6-angled, the apophysis tapering or short-cylindric but not sharply separated from the rest of the capsule by a deep basal constriction. The epiphragm is loosely attached and early deciduous. Capsules are pale greenish or yellowish brown rather than dark brown or purplish, and not glaucous when fresh as in *Polytrichum*. The exothecial cells are not bulging mammillose or pitted, but may have a diffuse thin spot on the outer wall. Spores are papillose rather than minutely echinulate as in *Polytrichum*. *Polytrichastrum alpinum* is distinct genetically from other members of the genus (G. S. Derda et al. 1999). Other *Polytrichastrum* species show evidence of allopolyploid origin, possibly involving interspecific or even intergeneric hybridization between species of *Polytrichastrum* and *Polytrichum*.

SELECTED REFERENCE Smith, Gary L. 1992. Notes on North American Polytrichaceae: *Polytrichastrum* G. Sm. Bryologist 95: 270–273.

1. Lamellae coarsely papillose; capsules terete, long-cylindric to ovate-cylindric to suborbicular.
 2. Lamellae margins entire in profile; exothecial cells without thin spot 1. *Polytrichastrum alpinum*
 2. Lamellae margins crenate in profile, the marginal cells crowned by a papillose knob; [exothecial cells with thin spots] 2. *Polytrichastrum papillatum*
1. Lamellae not papillose (rarely faintly striate-papillose); capsules 4–6-angled.
 3. Lamellae crenulate in profile.
 4. Marginal cells of lamellae in section narrow, pyriform, thickened in the narrowed apex 7. *Polytrichastrum appalachianum*
 4. Marginal cells of lamellae in section wider than those beneath, flat-topped or shallowly retuse 8. *Polytrichastrum pallidisetum*
 3. Lamellae entire in profile.
 5. Marginal lamina entire or obscurely denticulate, inflexed; leaf apex cucullate, rarely bluntly mucronate 3. *Polytrichastrum sexangulare*
 5. Marginal lamina toothed, plane or erect, not inflexed; leaf apex ending in a short awn.
 6. Marginal cells of lamellae in section wider than those beneath, transversely elliptic, the free wall conspicuously thickened, often brownish 6. *Polytrichastrum ohioense*
 6. Marginal cells of lamellae ovate to elliptic, usually slightly taller than wide, not or evenly thickened.
 7. Marginal lamina 5–9(–20) cells wide, somewhat incurved when dry; median sheath cells rectangular (3–5:1) 4. *Polytrichastrum longisetum*
 7. Marginal lamina 2–5 cells wide, ± erect; median sheath cells elongate (5–9:1) 5. *Polytrichastrum formosum*

1. *Polytrichastrum alpinum* (Hedwig) G. L. Smith,
Mem. New York Bot. Gard. 21(3): 37. 1971 [F]



Polytrichum alpinum Hedwig, Sp. Musc. Frond., 92, plate 19, fig. 2b. 1801; *Pogonatum alpinum* (Hedwig) Palisot de Beauvois

Plants very variable in size, small to robust, dull green or brownish green, reddish with age, in loose or compact tufts. **Stems** (1–)4–6 (–14) cm, densely leafy above, often leafless and thread-like below, simple or sparingly

to fasciculately branched. **Leaves** (4–)5–8(–19) mm, loosely to densely imbricate, erect-spreading and subtubulose when dry, erect-spreading and widely spreading when moist; sheath ± nitid, elliptic to obovate, with tapering shoulders (in var. *fragile* contracted above the sheath and the blade caducous), broadly hyaline-margined; blade linear-lanceolate, the apex narrowly acute to finely acuminate; marginal lamina 2–5 cells wide, erect, coarsely serrate with multicellular teeth, distantly serrulate to subentire; costa excurrent, ending in a short, brownish, toothed awn; lamellae 5–8 cells high, entire in profile, the marginal cells with the free wall appearing

greatly thickened, the marginal cells in section enlarged, yellowish to dark brown, ovate to narrowly ovate, the lateral walls strongly thickened, the lumen narrowly pentagonal and pointed at the apex, coarsely papillose; median cells of sheath 40–60(–80) × 6–12 μm, elongate-rectangular, thin-walled; cells of the marginal lamina 10–15 μm, subquadrate, sometimes transversely elongate; perichaetial leaves scarcely longer than the stem leaves. **Seta** (1–)3–5 cm, brownish. **Capsule** various, (1.5–)3–5(–8) mm, terete, narrowly cylindrical to oblong-cylindrical and curved, ovate-cylindrical, or ovoid to almost spherical, suberect to inclined to almost horizontal; hypophysis tapering, rugose, with numerous conspicuous stomata in a broad basal band; exothecial cells irregularly rectangular, not bulging or mammillose, thin spots absent, rather thick-walled; peristome 600 μm (teeth 150–250 μm), divided to 0.6–0.75, the teeth 45–50, with some teeth irregularly developed and unequal, pale to somewhat darker in the median line. **Spores** 14–20 μm.

Varieties 8 (4 in the flora): widely distributed in northern North America, and throughout cool temperate and boreal latitudes in the Northern Hemisphere, s temperate South America, Pacific Islands (New Zealand), Australia, Antarctica.

Polytrichastrum alpinum is highly variable in habit and plant size, dentition of the leaves, and capsule shape. However, all forms of the species are easily recognized by the entire-margined, coarsely papillose lamellae and terete capsules with smooth, non-pitted exothecial cells. The marginal cells of the lamellae in section are distinctive in shape and wall thickening, elegantly described by A. J. E. Smith (2004) as “strawberry-shaped.” The wall thickenings extend down the lateral walls, so that in profile the free margin appears to be much thicker-walled and the lumen more restricted than is actually the case. The marginal cells of *P. sexangulare* are similar in shape and wall thickening, but smooth. The only North American taxa of Polytrichaceae likely to be confused with *P. alpinum* when sterile are *Meiotrichum lyallii* and *Pogonatum urnigerum*. In *P. urnigerum* the marginal cells of the lamellae are shorter and broader at the apex with a pentagonal lumen; in *M. lyallii* the marginal cells seen in profile are irregularly striate and pitted rather than papillose.

1. Plants medium to robust; leaves sharply serrate; capsules short- to long-cylindrical.
2. Plants medium, (2–)4–6(–10) cm; leaves (4–)5–8 mm; capsule 3–5 × 0.8–1 mm, short-cylindrical or slender and subarcuate 1a. *Polytrichastrum alpinum* var. *alpinum*
2. Plants robust, to 14 cm; leaves 12–14(–19) mm; capsule 5–8 × 1.5–2.2 mm, often ± zygomorphic and widest below the middle 1b. *Polytrichastrum alpinum* var. *sylvaticum*

1. Plants small (1–2 cm); leaves entire to finely and remotely serrate toward the tip; capsules ovoid to subglobose.
3. Leaves not fragile, not constricted at junction of sheath and blade, the blade persistent 1c. *Polytrichastrum alpinum* var. *septentrionale*
3. Leaves fragile, constricted at the junction of sheath and blade, the blade caducous 1d. *Polytrichastrum alpinum* var. *fragile*

1a. *Polytrichastrum alpinum* (Hedwig) G. L. Smith var. *alpinum*

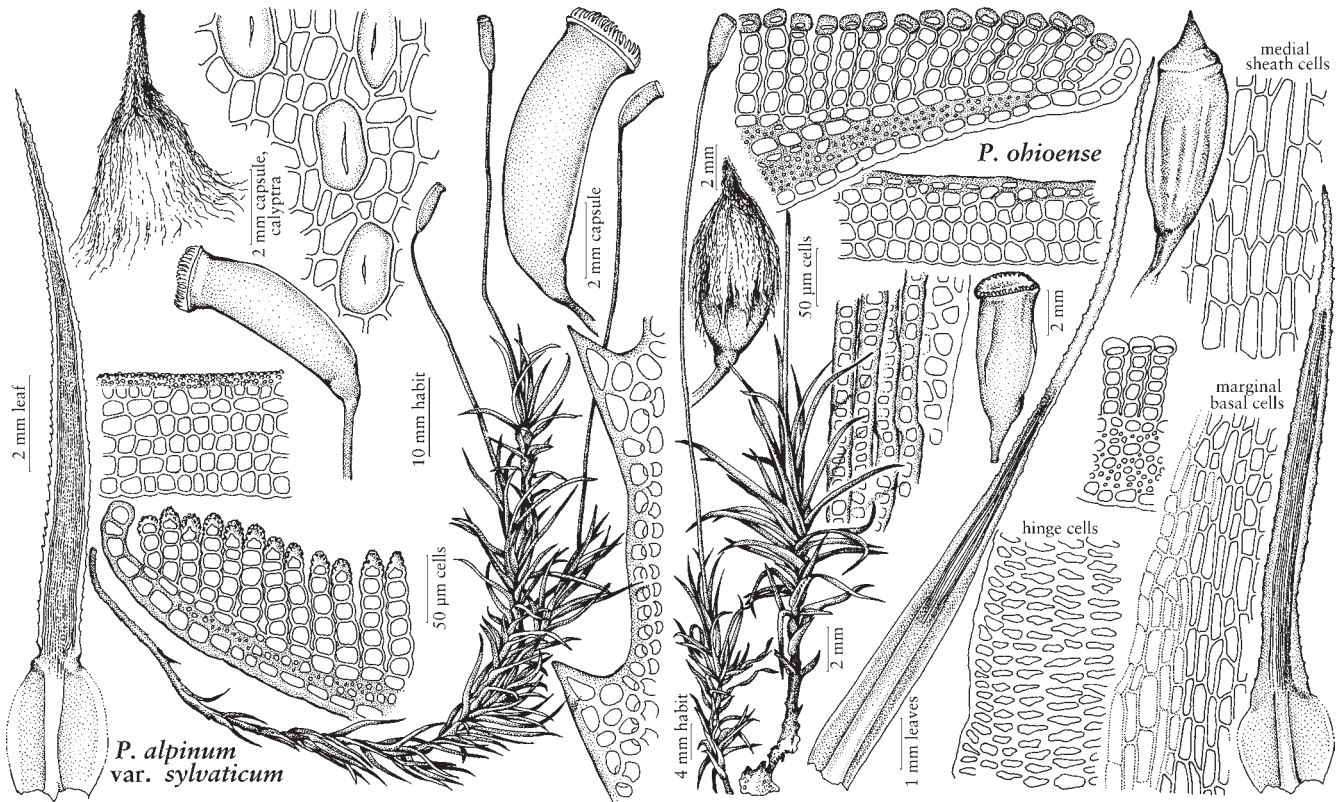


Polytrichum alpinum var. *arcticum* (Bridel) Wahlenberg; *Pogonatum alpinum* var. *brevifolium* (R. Brown) Bridel

Stems (2–)4–6(–10) cm, simple to fasciculately branched. **Leaves** (4–)5–8 mm, coarsely toothed. **Capsule** 3–5 × 0.8–1 mm, short-cylindrical to long-cylindrical and subarcuate.

Soil or humus, shaded non-calcareous rock outcrops, banks, and other shady situations; moderate to high elevations; Greenland; B.C., N.B., N.W.T., N.S., Nunavut, Ont., Que., Yukon; Alaska, Calif., Colo., Idaho, Maine, Mass., Mich., Minn., Mont., N.H., N.Mex., N.Y., N.C., Oreg., Pa., Vt., Wash., W.Va., Wis.; Mexico; temperate s South America; Europe (Turkey); n, c Asia (Japan, New Guinea); s Africa; Pacific Islands (New Zealand); Australia; Antarctica.

Variety *alpinum* is widely distributed across northern North America, growing in thick masses in crevices and ledges on moist, shaded rock outcrops, also common at all elevations in the Arctic, on tussocks in open tundra, stony banks, and outcrop ledges. In Nunavut, it is known from Bathurst Island and Ellesmere Island. Variety *arcticum* has traditionally been the repository for plants with cylindrical capsules (as opposed to the smaller, ovoid capsules of var. *septentrionale*) and probably comes closest to being “typical” *Polytrichastrum alpinum*. The common expression of *P. alpinum* in eastern North America has a distinctive aspect, tall and gracile, with slender, subtubulose leaves, and elongate, slender, distinctly curved and inclined capsules (G. E. Nichols 1937), and has no exact counterpart among the traditionally recognized varieties of the species. *Polytrichum alpinum* var. *brevifolium* has a more northerly distribution and is smaller in all its parts, but has the toothed leaves and cylindrical capsule of the typical form.



POLYTRICHASTRUM

1b. Polytrichastrum alpinum var. *sylvaticum*

(Menzies) G. L. Smith, Sida 22: 547. 2006 [E] [F]



Polytrichum sylvaticum Menzies, Bot. Zeitung (Regensburg) 1: 74. 1802; *Pogonatum alpinum* var. *macounii* (Kindberg) Cardot & Thériot; *P. macounii* (Kindberg) Kindberg & Macoun; *Polytrichum alpinum* var. *campanulatum* (Hornschnuch) Müller Hal.; *P. alpinum* var. *sylvaticum* (Menzies) Lindberg

Stems to 14 cm, simple or sparingly branched. **Leaves** (9–)12–14(–19) mm, coarsely toothed. **Capsule** 5–8 × 1.5–2.2 mm, often ± zygomorphic and widest below the middle, suberect to inclined to almost horizontal.

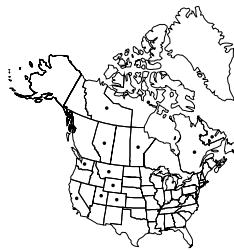
Soil, moist woods; low to moderate elevations (to 1400 m); B.C.; Alaska, Oreg., Wash.

Variety *sylvaticum* is a robust plant of the Pacific Northwest with stems to 14 cm high, sharply serrate leaves to as much as 19 mm, and large, plump, cylindric capsules, often ± zygomorphic. The type was collected by Menzies somewhere on the Northwest coast; *Pogonatum macounii* was collected in a ravine at 1370 m on Vancouver Island. *Polytrichum alpinum* var. *campanulatum* has large, ovoid-gibbous, almost

horizontal capsules and is probably distinct, but its distribution is poorly understood.

1c. Polytrichastrum alpinum var. *septentrionale*

(Bridel) G. L. Smith, Mem. N.Y. Bot. Gard. 21(3): 37. 1971



Polytrichum septentrionale Bridel, J. Bot. (Schrader) 1800(1): 285. 1801; *Pogonatum alpinum* var. *septentrionale* (Bridel) Bridel; *Polytrichum alpinum* var. *septentrionale* (Bridel) Lindberg; *P. norwegicum* Hedwig

Stems to 2 cm, slender and wiry, in dense tufts. **Leaves** densely imbricate, not fragile, channeled and incurved when dry, scarcely spreading when moist; not constricted at junction of sheath and blade, the blade persistent, sheath broadly elliptic; marginal lamina typically entire, or finely and remotely serrate toward the tip. **Capsule** small and subglobose.

Soil; moderate to high elevations; Alta., Man., Nfld. and Labr. (Labr.), N.W.T., N.S., Nunavut, Que.; Calif., Colo., Mont., Utah, Wash., Wyo.; Europe; n Asia.

Variety *septentrionale* is an arctic-alpine taxon. In arctic North America there is a correlation between

capsule shape and leaf serration, plants with distinctly serrate leaves having ovoid-cylindric or cylindric capsules, whilst those with entire or subentire margins have subglobose or ovoid capsules (D. G. Long 1985).

1d. *Polytrichastrum alpinum* (Hedwig) G. L. Smith var. ***fragile*** (Bryhn) D. G. Long, Meddel. Grønland, Biosci. 17: 30. 1985



Polytrichum fragile Bryhn, Bryoph. Itin. Pol. Norv., 122, plate 122, fig. 3. 1906; *Pogonatum alpinum* var. *fragile* (Bryhn) H. A. Crum; *Polytrichum alpinum* var. *fragile* (Bryhn) Nyholm

Stems 1–2 cm, in compact tufts. **Leaves** fragile, constricted at the junction of sheath and blade, the

blade caducous; marginal lamina entire, rarely distantly serrulate. **Capsule** ovoid or subglobose.

Growing where subject to periodic inundation, wet meadows, springs and lake margins, occasional in open tundra, beach ridges and roadside banks, low elevations; Greenland; N.W.T., Nunavut; Alaska; Europe (n Scandinavia); Asia (Russia in Siberia).

Variety *fragile* is a distinctive taxon of the high Arctic with regularly caducous leaves, in North America common only in arctic Alaska on the coastal plain to 100(–800) m, with scattered records throughout arctic Canada (D. G. Long 1985). In Nunavut, it is known from Baffin Island, Ellesmere Island, and Melville Island.

2. *Polytrichastrum papillatum* G. L. Smith, J. Hattori Bot. Lab. 38: 633, figs. 12–24. 1974



Polytrichum papillatum (G. L. Smith) L. E. Anderson, H. A. Crum & W. R. Buck

Plants slender, with the aspect of *P. alpinum* var. *septentrionale*. **Stems** to 2 cm, leafless below, leafy above. **Leaves** channeled and incurved when dry, spreading when moist, narrowly triangular,

from a broadly elliptic, hyaline-margined sheathing base; marginal lamina serrate to almost entire; lamellae 5–6 cells high, crenate in profile, with each cell crowned by a papillose knob, the marginal cells in section pyriform. [**Seta** to 1.5 cm, curved. **Capsule** subspherical; exothecial cells with a distinct thin spot; peristome teeth ca. 40, hyaline, now and then compound.]

Substrate and elevation undetermined; Alaska; Asia (Kashmir, e Nepal).

Polytrichastrum papillatum is known in North America from a single, sterile collection from southern Alaska (Valdez), collected by F. J. Hermann, but is

possibly more widespread and overlooked. The marginal cells of the lamellae are coarsely papillose, and resemble those of *P. alpinum* in section. In profile, however, the lamellae are crenate, the marginal cells crowned by a papillose knob. The exothecial cells with a pale but distinct thin spot in the outer wall further distinguish this species from *P. alpinum*.

3. *Polytrichastrum sexangulare* (Bridel) G. L. Smith, Mem. New York Bot. Gard. 21(3): 37. 1971



Polytrichum sexangulare Bridel, J. Bot. (Schrader) 1800(1): 285. 1801

Plants small to medium, rather wiry, dark green to reddish brown with age. **Stems** 1–3(–6) cm, simple, erect or decumbent, the cortical cells thin- or thick-walled. **Leaves** 3–6 mm, loosely to densely imbricate, erect-incurved at the

tips and appressed to the stem when dry, erect-spreading when moist, obtusely cucullate, often secund; sheath broadly elliptic, hyaline-margined, gradually tapering or abruptly contracted to the blade; blade lanceolate to ligulate, almost tubular when dry; costa percurrent or slightly excurrent, cucullate at the apex, rarely bluntly mucronate; marginal lamina 2–6 cells wide, entire to obscurely denticulate, slightly broader and inflexed in the distal part of blade, covering the lamellae; lamellae 5–8(–11) cells high, minutely crenulate in profile, the marginal cells in section larger than those beneath, narrowly ovate to pyriform, smooth or very rarely indistinctly papillose; median sheath cells elongate-rectangular, (18–)24–40 × 8–10(–18) μm; cells of marginal lamina 11–15 μm, quadrate to short rectangular, ± equally thick-walled; perichaetial leaves slightly longer than the foliage leaves. **Seta** 1.5–3 cm, rather stout, straight or arcuate with age. **Capsule** 2–3 mm, short-cylindric to ovoid to globose, bluntly (4–)5–6-angled to terete, erect to horizontal to nodding; hypophysis small, scarcely delimited, stomata large and scattered on the proximal 1/3 of the urn; exothecium smooth, the cells variable in shape, trigonal to hexagonal, with a diffuse thin spot; peristome pale 220–300 μm high, divided to 0.3–0.5, the teeth 50–64, slender, of uniform size, or short triangular, the alternate teeth smaller. **Spores** 16–18 μm.

Varieties 2 (2 in the flora): cool temperate and boreal Northern Hemisphere.

There has been a long-standing confusion of the names *Polytrichum septentrionale*, *Polytrichastrum norwegicum*, and *Polytrichastrum sexangulare* dating from the earliest days of bryology, and still met with in older collections in herbaria. Hedwig's *Polytrichastrum norwegicum* was briefly in vogue as a name for this species, but the type of *Polytrichastrum norwegicum* is a form of *Polytrichastrum alpinum* (Gary L. Smith 1971).

1. Stem cortical cells thin-walled; seta straight; capsule short-cylindric to ovoid to subglobose, (4-)5-6-angled; peristome teeth 50-64, slender, of uniform size 3a. *Polytrichastrum sexangulare* var. *sexangulare*

1. Stem cortical cells thick-walled; seta rather thick and curved; capsule subglobose, terete; peristome teeth 32, attenuate, of unequal size 3b. *Polytrichastrum sexangulare* var. *vulcanicum*

3a. *Polytrichastrum sexangulare* (Bridel) G. L. Smith var. *sexangulare*



Plants small to medium, in loose tufts. **Stems** with cortical cells thin-walled. **Leaves** loosely to densely imbricate, erect-incurved at the tips, often ± secund, obtusely cucullate; sheath broadly elliptic, contracted to the blade; marginal lamina 2-6 cells wide, slightly broader and inflexed in the distal

part of blade; perichaetial leaves similar to the foliage leaves. **Seta** straight. **Capsule** (4-)5-6-angled to terete; short-cylindric to ovoid to subglobose; peristome teeth 50-64, slender, of uniform size.

Damp gravelly soil and rocks, snowbed communities and beside snow-melt streams; moderate to high elevations; Greenland; Alta., B.C., Nfld. and Labr., N.W.T., Nunavut, Que., Yukon; Alaska, Mont., Utah, Wash., Wyo.; Europe; Asia (Japan, Russia in s Siberia); Atlantic Islands (Iceland).

In Nunavut, var. *sexangulare* is known from Baffin Island. Even when sterile, it can usually be recognized by secund, tubulose leaves with an obtusely cucullate apex. *Polytrichastrum alpinum* var. *septentrionale* is similar, but has papillose lamellae, and the leaf apex is not cucullate.

3b. *Polytrichastrum sexangulare* var. *vulcanicum* (C. E. O. Jensen) G. L. Smith, Bryologist 95: 270. 1992



Polytrichum sexangulare var. *vulcanicum* C. E. O. Jensen, Bot. Tidsskr. 20: 109. 1896; *Pogonatum sphaerothecium* Bescherelle; *Polytrichum sphaerothecium* (Bescherelle) Müller Hal.

Plants small, forming large brownish mats. **Stems** with 5-6 layers of thick-walled cortical cells.

Leaves incurved and closely appressed to the stem when dry, erect-spreading when moist; sheath poorly delimited; marginal lamina expanded and involute, covering the lamellae; perichaetial leaves abruptly narrowed to the

blade. **Seta** arcuate with age. **Capsule** nearly globose, horizontal to nodding; peristome teeth 32, short, attenuate, the alternate teeth often smaller.

Volcanic rocks; high elevations; B.C.; Alaska; e Asia (Japan); Atlantic Islands (Iceland).

Variety *vulcanicum* is notable for the rather thick, curved seta, nodding, globose capsule, and the stem cortex composed of very thick-walled cells, in contrast to the thin-walled cortex of var. *sexangulare*. It is probably best considered a variety of *P. sexangulare*, despite its distinctive peristome and the absence of capsule angles. E. Lawton (1971) described intermediate forms in British Columbia with acute-tipped leaves and angled capsules, but with the stem cortical cells and peristome of var. *vulcanicum*.

4. *Polytrichastrum longisetum* (Bridel) G. L. Smith, Mem. New York Bot. Gard. 21(3): 35. 1971



Polytrichum longisetum Bridel, J. Bot. (Schrader) 1800(1): 286. 1801; *P. formosum* var. *aurantiacum* (Bridel) C. J. Hartman; *P. gracile* Menzies; *P. gracile* var. *anomalum* (Milde) I. Hagen

Plants medium to large, mostly unbranched, dark green, in loose tufts. **Stems** 2-5(-10) cm. **Leaves**

5-10 mm, somewhat contorted and flexuose when dry, spreading-recurved when moist; sheath short, oblong, yellowish (in what has been known as *Polytrichum gracile* var. *anomalum*) weakly differentiated and tapering to the blade, hyaline margined, the hinge-tissue often not well developed; blade narrowly lanceolate; marginal lamina typically broad and often somewhat inflexed, 5-9(-12) cells wide (to 20 cells wide in var. *anomalum*), plane to erect, sharply toothed nearly to the sheath, the teeth composed of a single, elongate tooth cell, or at times less strongly toothed to denticulate; costa excurrent, ending in a short awn; lamellae in profile entire or finely serrulate, 3-7 cells high, the marginal cells in section ovate to elliptic, scarcely enlarged, usually taller than wide, sometimes slightly thicker-walled, smooth; sheath cells short-rectangular, (30-)40-60 × 14-18 μm (ca. 3-4:1); cells of the marginal lamina 15-18 μm (larger in var. *anomalum*), quadrate to transversely elongate; perichaetial leaves similar to the vegetative leaves or slightly larger. **Seta** 4-7 cm tall, typically exceeding the leafy shoots in length, yellowish, reddish brown below. **Capsule** 3-5 mm, slender to ovoid, (4-)5-6-angled, yellowish brown; hypophysis cylindric, narrower than the urn; exothecium smooth, the cells irregularly rectangular, not bulging, without thin spots; peristome pale, 400-600 μm, divided to 0.8, the teeth ca. 50, somewhat irregular in size and shape, rather slender. **Spores** 18-28 μm.

Moist acidic to basic peaty sites, hummocks, meadows and wet tundra (D. G. Long 1985); moderate to high elevations; Greenland; Alta., B.C., Man., N.B., Nfld. and Labr., N.W.T., N.S., Ont., Que., Sask.; Alaska, Colo., Ill., Minn., Mont., N.Y., Pa., Wis., Wyo.; s temperate South America; Europe; n Asia (Japan, Korea, New Guinea); Pacific Islands (New Zealand).

Polytrichastrum longisetum is a circumpolar boreo-temperate species, and is also found in the Southern Hemisphere. In northern Europe, the species occurs on well-drained acidic soil in heaths and moorlands, also in woods; the seta is often conspicuously longer than the leafy shoots (whence the name), and the capsules broadly ovoid, widest below the middle. As represented in eastern North America, *P. longisetum* is similar in habit and habitat to *P. formosum* var. *densifolium* and *P. pallidisetum*, but differs in the less strongly differentiated leaf sheath, short-rectangular sheath cells, and broad marginal lamina. Both *P. formosum* and *P. longisetum* have the marginal cells of the lamellae scarcely differentiated, in profile entire to finely serrulate by the projecting leading angles of the marginal cells; in *P. pallidisetum* the lamellae are crenulate in profile, and the marginal cells in cross-section broadened, flat-topped to shallowly retuse. Specimens identified as *Polytrichum gracile* var. *anomulum*, found in the wettest habitats, even submerged, are sometimes startlingly *Atrichum*-like in appearance. The leaf sheath is weakly developed and scarcely broader than the blade, the 1-stratose lamina is up to 20 cells wide, and the lamellae are few in number and confined to the median portion of the blade.

5. *Polytrichastrum formosum* (Hedwig) G. L. Smith, Mem. New York Bot. Gard. 21(3): 37. 1971



Polytrichum formosum Hedwig, Sp. Musc. Frond., 92, plate 19, fig. 1a. 1801; *P. attenuatum* Menzies

Plants medium and slender to large and robust, green to dark olive green to blackish, in loose tufts. **Stems** (2-)3-8(-20) cm, mostly unbranched. **Leaves** 6-8 (-12) mm, erect to erect-spreading

when dry, spreading to subsquarrose and broadly recurved when moist; sheath ovate to elliptic, yellowish, hyaline-margined, gradually tapering or abruptly contracted to the blade, the cells at the shoulders forming a differentiated hinge; blade lanceolate to linear; costa prominent abaxially and toothed near the tip; excurrent as a short, toothed point; marginal lamina erect, (2-)3-5(-10) cells wide, plane or erect, sharply toothed from apex nearly to the sheath; lamellae (3-)4-5(-7) cells high, margins ± entire to finely serrulate in profile, the marginal cells in section rounded to narrowly elliptic and somewhat taller than the cells beneath, the cell walls not or

moderately thickened; median cells of sheath 8-12 µm wide, narrowly rectangular, 5-7(-10):1; cells of marginal lamina subquadrate, 10-15 µm. **Sexual condition** dioicous or polygamous; perichaetial leaves similar to the foliage leaves, or somewhat longer, with a longer sheath. **Seta** 3-6 cm, yellowish to reddish brown. **Capsule** 4-7 mm, rather slender or short-rectangular, acutely 4(-6)-angled, inclined to almost horizontal, pale yellowish brown to brownish; hypophysis cylindric, indistinctly delimited or set off by a shallow groove; exothecium smooth or the cells weakly convex, quadrate to hexagonal, without a central thin spot; peristome 600 µm, divided to 0.6, the teeth 64 and highly regular in form or fewer and somewhat irregular, pale to brownish; epiphragm absent marginal teeth. **Spores** 12-16 µm.

Varieties 3 (2 in the flora): widespread, temperate to cool temperate latitudes in the Northern Hemisphere.

European treatments often assert a similarity between *Polytrichastrum formosum* and *Polytrichum commune*, which cannot be said of the North American expression of the species. The habitat and ecology of the European plants are also distinct: A. J. E. Smith (2004) described *P. formosum* in Britain as a common and weedy species of heaths, moorland, woods, outcrops, and old walls.

1. Plants often robust, 5-10(-20) cm; leaves subsquarrose and broadly spreading- recurved when moist; lamellae 5-7 cells high, entire, the marginal cells in section rounded, moderately thick-walled; capsule short rectangular; hypophysis delimited by a shallow groove; peristome teeth 64, regular in form; dioicous 5a. *Polytrichastrum formosum* var. *formosum*

1. Plants rather slender, 3-6(-10) cm; leaves spreading when moist; lamellae (3-)4-6 cells high, the marginal cells narrowly elliptic, not or only slightly thickened; capsule slender; hypophysis not sharply delimited; peristome teeth 50-64, somewhat irregular in size and shape; monoicous (polygamous) 5b. *Polytrichastrum formosum* var. *densifolium*

5a. *Polytrichastrum formosum* (Hedwig) G. L. Smith var. *formosum*



Plants medium to large and robust. **Stems** 5-10(-20) cm. **Leaves** 6-12 mm, subsquarrose and broadly spreading-recurved when moist; marginal lamina 2-5 cells wide, erect; lamellae 5-7 cells high, entire, the marginal cells rounded and ± thick-walled. **Sexual condition** dioicous. **Capsule** short rectangular, yellowish to brownish; hypophysis cylindric, delimited by a shallow groove; peristome teeth 64, very regular in form.