

BFNA Title: Scapaniaceae
Author: Provisional Publication
Date: Dec. 4, 2020
Edit Level: S
Version: 1

Bryophyte Flora of North America, Provisional Publication
Missouri Botanical Garden
BFNA Web site: <http://www.mobot.org/plantscience/BFNA/bfnamenu.htm>

[Notice](#)

[Return to Home](#)

XX. SCAPANIACEAE Migula

Alan T. Whittimore

Plants forming mats or turfs or spreading from substrate; branches sometimes intercalary from sides of stem, sometimes replacing ventral half of a leaf; usually without flagella. **Leaves** alternate, succubous, sometimes succubous ventrally and transverse or incubous dorsally, plane, concave, or folded, always lobed, entire or toothed; underleaves very rarely present on sterile shoot sectors. **Rhizoids** scattered over ventral stem. **Specialized asexual reproduction** by 1--2(--3)-celled gemmae, common on margins of ordinary leaves. **Gynoeceum** terminal on an ordinary leafy branch. **Perianth** with or without subfloral branches, well developed, cylindrical and smooth or plicate or flattened, mouth wide or somewhat narrowed, perigynium absent.

Genera ca. 35, species ca. 350 (15 genera, 114 species in the flora): cosmopolitan, except Antarctica.

Scapaniaceae is one of the largest families of liverworts, found worldwide but speciose in cool-temperate to arctic regions of the Northern Hemisphere. Species of Scapaniaceae form an important part of the vegetation in arctic, boreal, and high-altitude floras around the Northern Hemisphere.

The name Scapaniaceae was originally used only for the group of genera with leaves sharply folded together along a median keel (*Scapania*, *Diplophyllum*, *Macrodiplrophyllum*, and *Douinia*). This is virtually the only grouping in the broad family that is well-defined and recognizable. The bulk of the species in the family have plane or concave leaves and were traditionally placed in a separate family Lophoziaceae. These species show highly homoplasious morphologies, and groups are poorly defined at best. These taxa have been studied by a series of experienced taxonomists (K. Müller, H. Buch, S. Arnell, R. M. Schuster, R. N. Schljakov, K. Damsholt, N. A. Konstantova, L. Söderström, V. Bakalin), but there has been no consensus about generic delimitation in the family—most treatments have delimited genera in the groups differently. The recent availability of chloroplast and ITS sequence data has provided little clarity. Results have been partly inconsistent among DNA sequence studies, and statistical support for many clades (especially the crucial basal clades) is weak to none. It is impossible to discuss here all the different generic concepts that have been applied in this family. Some

species have been placed in four or five different genera over a span of 30--40 years. Virtually every author presents different generic concepts, and none of them is well supported.

At the same time, the overall classification and patterns of variation are not well presented in the recent literature. Aside from a few important flora treatments (K. Damsholt 2002; J. A. Paton 1999a, b; R. M. Schuster 1969, 1974; R. N. Shlyakov 1980, 1981) there are no broad, synthetic treatments of generic classification in the family newer than the revision of R. M. Schuster (1951); the literature since then consists of large numbers of short papers covering small parts of the problem, publications presenting new nomenclature with little information on variation and evolution in the group, and checklists.

The chloroplast DNA phylogeny of R. T. de Roo et al. (2007) placed Cephaloziellaceae in the middle of Scapaniaceae. In response to this, L. Söderström et al. (2010) split Scapaniaceae into two morphologically indistinguishable families, Scapaniaceae s. str. and Anastrophyllaceae, and also transferred some Scapaniaceae species to Cephaloziellaceae. However, these groupings were very poorly supported in de Roo's analysis, with several taxa appearing in different clades in their parsimony and Bayesian analyses of the same data set. The surprising placement of Cephaloziellaceae was not well supported in their analysis, and later studies have not supported it: subsequent studies have found that Cephaloziellaceae is either sister to Scapaniaceae s. lat. (J. Hentschel et al. 2007, K. Feldberg et al. 2013, B. Shaw et al. 2015), or that the position of Cephaloziellaceae is highly unstable, varying drastically in different analyses of the same dataset (A. A. Vilnet et al. 2012). The unexpected position of Cephaloziellaceae in R. T. de Roo et al. (2007) seems to be a result of long branch attraction, and not a true indicator of relationships, so the transfer of Scapaniaceae species to Cephaloziellaceae and the recognition of a family Anastrophyllaceae do not seem appropriate.

Chloroplast sequences show that north temperate and Arctic taxa do seem to fall into two clades, corresponding to the two families of L. Söderström et al. (2010), but tropical and southern hemisphere taxa don't seem to fall into either of these groups, some taxa move from one group to another depending on the analysis (at least in R. T. de Roo et al. 2007), statistical support is lacking for most putative clades, and no morphological differences between them, so at this time, there is no firm ground for recognizing two or more families here.

The generic definitions used by FNA authors here will doubtless be criticized by some. A more complete analysis, with more extensive sampling of taxa worldwide and utilizing many nuclear loci instead of one or none, will be required before a stable classification can be published.

SELECTED REFERENCES: Feldberg, K., J. Heinrichs, A. R. Schmidt, J. Vana, and H. Schneider. 2013. Exploring the impact of fossil constraints on the divergence time estimates of derived liverworts. *Plant Systematics and Evolution* 299: 585--601. Schuster, R. M. 1951. Notes on Nearctic Hepaticae III. A Conspectus of the Family Lophoziaceae, with a Revision of the Genera and Subgenera (*American Midland Naturalist* 45(1): 1--117. Stotler, R. E. and B. Crandall-Stotler. 2017. *Ann. Missouri Bot. Gard.* 102: 574--709. Vilnet, A. A., A. N. A. Konstantinova, and A. V. Troitsky. 2012. Molecular phylogeny and systematics of the suborder Cephaloziineae with special attention to the family Cephaloziaceae s.l. (Jungermanniales, Marchantiophyta). *Arctoa* 21: 113--132.

1. Leaves sharply folded along the midline, ventral half of leaf insertion succubous, dorsal half clearly incubous.
 2. Leaf lobes lanceolate, acute to acuminate. 12. *Douinia*
 2. Leaf lobe oblong to ovate or almost circular, broadly acute to rounded.
 3. Gemmae smooth (rarely angular); lobes of leaf mostly ovate to elliptical or almost circular; perianth dorsiventrally flattened, smooth. 15. *Scapania*
 3. Gemmae stellate, angular, rounded polygonal; lobes of leaf lingulate, +/- parallel-sided; perianth cylindrical, plicate, narrowed to mouth.
 4. Cell walls in midleaf usually +/- uniformly thickened; gemmae 1--2-celled, stellate with strongly protuberant angles; leaves never ventrally decurrent; leafy shoots 1--3.5 mm wide. 13. *Diplophyllum*
 4. Cell walls in midleaf usually thin but with large trigones; gemmae 2--4-celled, angular, rounded polygonal or ovate; leaves ventrally decurrent or not; leafy shoots 2--4.5 mm wide. 14. *Macrodiplphyllum*
1. Leaves plane or concave but never sharply folded, dorsal half of leaf insertion succubous or transverse.
 5. Leaves unlobed. 4. *Biantheridion*
 5. Leaves 2--4-lobed.
 6. Leaves lobed 0.6--0.8 of their length, lobes strongly channelled, leaf bases and sometimes lobe margins strongly toothed or ciliate.
 7. Leaves symmetrically 4-lobed, transversely inserted or nearly so; plants rusty brown. 1. *Tetralophozia*
 7. Leaves asymmetrically 2--3-lobed, dorsal lobe clearly larger than ventral lobe, leaf clearly succubous; plants golden yellow-brown. 2. *Plicanthus*
 6. Leaves lobed 0.2--0.5(--0.7) of their length, lobes plane or only weakly channelled; margins entire or irregularly toothed or with cilia only at the ventral base; green, brown, or red.
 7. Leaves 3--4-lobed.
 8. Dorsal half of leaf insertion transverse, ventral half succubous. Leaves 3-lobed, very asymmetrical, dorsal lobe much smaller than ventral lobe. 11. *Tritomaria*
 8. Leaf insertion succubous throughout. Leaves 2--4-lobed, scarcely asymmetrical, dorsal lobe similar to ventral lobe.
 9. Plants +/- soft and succulent; leaves 2--3(--4)-lobed; oil-bodies in the leaf cells 5--50 per cell. 8. *Schistochilopsis*
 9. Plants firm, not succulent; leaves 3--4-lobed; oil-bodies in the leaf cells 3--8(--12) per cell. 3. *Barbilophozia*
 7. Leaves 2-lobed.
 10. At least dorsal half of leaf leaf transversely inserted.
 11. Underleaves present (at least in parts of the stem), 2-lobed or ciliate; leaf bases sometimes ciliate; plants erect or ascending; leaves deeply concave. 3. *Barbilophozia*

11. Underleaves absent or rudimentary (present and unlobed in *Lophozia heteromorpha*); leaf bases entire or toothed; plants prostrate to ascending; leaves plane to concave.
12. Leaves soft, plane or weakly concave, lobe margins toothed; stems very fleshy, 0.4--1.1 mm wide. 8. *Schistochilopsis*
12. Leaves entire except for the two lobes, firm, concave or canaliculate; stems firm, (0.035--0.05--0.4 mm wide.
13. Leaves 2-lobed 0.5--0.8 of length, insertion transverse throughout. 10. *Sphenolobopsis*
13. Leaves 2-lobed 0.1--0.3 of length, dorsal half of leaf insertion transverse, ventral half succubous. 9. *Anastrophyllum*
10. Leaf insertion succubous throughout.
14. Ventral margin of leaf broadly reflexed; stems erect, 30--90 mm long. 7. *Anastrepta*
14. Ventral margin of leaf not reflexed; stems usually creeping, if erect then shorter.
15. Perianth smooth, easily detached; female bracts not enveloping base of perianth; lobes of leaves rounded; gemmae absent. 6. *Gymnocolea*
15. Perianth plicate, persistent; female bracts closely enveloping base of perianth; lobes of leaves acute (except *L. obtusa*); gemmae often present.
16. Plants +/- soft and succulent; stems very fleshy, 0.4--1.1 mm wide; leaves 2---3(---4)-lobed; gemmae stellate or ellipsoidal. 8. *Schistochilopsis*
16. Plants firm, not succulent; stems firm, 0.1--0.5 mm wide; leaves mostly 2-lobed; gemmae angular. 5. *Lophozia*

1. TETRALOPHOZIA (R.M. Schuster) Schljakov, Novosti Sist. Nizsh. Rast. 13: 227. 1976 *
[Greek *tetra*, four, and genus *Lophozia*, alluding to the 4-fid lateral leaves]

E. Urmi

Chandonanthus subg. *Tetralophozia* R.M. Schuster, J. Hatt. Bot. Lab. 23: 206. 1960

Plants simple or sparingly branched, shoot tips often anticly bent, creeping among other foliose hepatics, ascending in loose mats, or +/- upright in tightly packed cushions, ocher or brown, rarely green. **Stems** with ventral- and lateral-intercalary branches, rarely terminally branched (*Frullania*-type); cell walls in transverse section +/- thickened, the surface wall of the epidermis the thickest, cell size gradually increasing from periphery to center; paraphyllia lacking except for gametangia; rhizoids hyaline, few or many, dependent on habit. **Lateral leaves** subtransversely inserted, succubous, imbricate or contiguous, hardly different in wet and dry condition, uneven, symmetrically divided in 4 lobes to more than half leaf length; lobes

triangular, canaliculate, the margins coarsely and spinosely toothed or ciliate; basal cells +/- elongated, lobe cells less so, all with distinct trigones often bulging, surface verruculose; oil bodies few per cell, botryoidal. **Underleaves** similar to lateral leaves, but a little smaller, 2-fid, and with narrower lobes. **Specialized asexual reproduction** rare (known only in *T. setiformis*), 1--2-celled gemmae on leaf margins. **Sexual condition** dioicous. **Androecia** intercalary, exactly as wide as vegetative parts (easily overlooked), number of bracts per androecium obviously indefinite (1--20), bracts similar to lateral leaves, but less deeply divided and somewhat saccate at base, bracteoles not bearing antheridia, antheridia (1--)2(--4) per bract, white or somewhat reddish, jacket cells not clearly tiered, 1 or 2 cell rows in antheridial stalk. **Gynoecia** terminal on long shoots, usually with 1 ventral-intercalary innovation, bracts and bracteole hardly differentiated; perianth longly exserted, +/- cylindric and often antically curved, strongly plicate, mouth lobed and ciliate. **Sporophytes** rather large. **Seta** transverse section with many homogeneous cells. **Capsule** black, ellipsoid, dehiscent with 4 lobes, wall layers 4, outer and innermost layer with brown nodular thickenings along the cell walls. **Elaters** free, 2-spiral. **Spores** spherical, brown.

Species 4 (2 in the flora); North America, Arctic, Europe, Asia, Africa.

SELECTED REFERENCES: Godfrey, J. D. and G. A. Godfrey, 1978. Asexual reproduction in *Chandonanthus setiformis*. Bryologist 81: 326--330. Laine, T. 1970. Notes on *Chandonanthus* Mitt. subg. *Tetralophozia* Schuster. Ann. Bot. Fenn. 7: 163--169. Schuster, R.M. 1966--1992. The Hepaticae and Anthocerotae of North America east of the hundredth meridian. 6 vol. (*Chandonanthus* in vol. 2: 241--252). Schuster, R.M. 2002. Revisionary studies of the Chandonanthoideae (Jungermanniales, Jungermanniaceae). Nova Hedwigia 74: 465--496. Urmi, E. 1983. *Tetralophozia filiformis* (Steph.) comb. nov. in Europa. J. Bryol. 12: 393--401.

1. Well developed shoots rarely more than 4 cm and seldom wider than 0.6 mm; lateral leaves with narrowly triangular lobes always more than twice as long as wide; lobes abaxially canaliculate, their margins abaxially recurved; fully developed perianths less than 1.5 mm
..... 1. *Tetralophozia filiformis*

1. Well developed shoots often 5--10 cm and often 0.6 mm or more in width; lateral leaves with broadly triangular lobes less than twice as long as wide; lobes abaxially concave, their margins incurved towards the stem; fully developed perianths longer than 1.5 mm
..... 2. *Tetralophozia setiformis*

1. *Tetralophozia filiformis* (Stephani) Urmi, J. Bryol. 12: 394

Chandonanthus filiformis Stephani, Sp. Hepat. 3: 645. 1909

Plants 3--20 (--40) x (0.1--)0.2--0.6(--0.9) mm, as +/- dense mats or cushions, yellowish or greenish brown. **Stems** (50--)100--150 μ m wide, with ventral or lateral intercalary branches; cells with +/- thickened walls; paraphyllia lacking; rhizoids if any, in loose groups closely proximal to underleaves, hyaline. **Lateral leaves** mostly imbricate, uneven, sometimes spreading, (0.1--)0.2--0.5 x 0.2--0.9 mm, hand-like, very deeply divided in four lobes, sinuses dorsally protruding, antical margin often with a very large tooth; lobes narrowly ovate and

acute, more than twice as long as wide, abaxially canaliculate; cells +/- elongated (except for marginal ones), subbasal cells 12--24(--32) x 10--17 μm , surface verruculose, with trigones (near leaf base bulging); oil bodies 3--5 per cell. **Underleaves** similar to lateral leaves, 2-fid and with narrower lobes. **Androecia bracts** less deeply divided than lateral leaves, less dentate, antheridial stalk uniseriate, jacket cells somewhat tiered. **Perianths** when fully developed less than 1.5 mm. **Sporophytes** not seen in region of flora.

Shaded siliceous rock outcrops in the Pacific rain forest with high air humidity, often on a thin layer of rather wet soil with dead organic material, sometimes on dead wood or even epiphytic on tree bases, often admixed with *Anastrophyllum minutum*, *Bazzania* sp., *Dicranum fuscescens*, *Diplophyllum taxifolium*, and *Scapania bolanderi*, occasionally with *Tetralophozia setiformis*; low to moderate elevations (0--600 m); B.C.; Europe; Asia.

Tetralophozia filiformis shows a highly disjunctive distribution. Its American population is at a distance of 5500 km from the E-Asian ones in Siberia and of 8000 km from the European.

2. *Tetralophozia setiformis* (Ehrhart) Schljakov, Novosti Sist. Nizsh. Rast. 13: 228. 1976

Jungermannia setiformis Ehrhart, Hannover. Mag. 22, 8: 142. 1784; *Chandonanthus setiformis* (Ehrhart) Lindberg; *Temnoma setiforme* (Ehrhart) Howe; *Tetralophozia setiformis* var. *alpina* (Hook.) L. Söderstr.

Plants (5--10--40(--150) x (0.2--0.5--0.8(--1) mm, longer plants sometimes sympodial by innovations, wiry and brittle when dry, in low mats or in densely packed cushions, ochre, brown, or rarely green. **Stems** mostly 200 μm wide, but from 80 to 300 μm , branching lateral- and ventral-intercalary, rarely terminal; cells somewhat thickened, those of medulla porose; paraphyllia lacking (except for androecia); rhizoids if any, in loose groups closely proximal to underleaves, hyaline. **Lateral leaves** imbricately overlapping, very uneven, base spreading but lobes upright and parallel to the stem, deeply and symmetrically divided in four lobes, sinuses abaxially protruding, antical margin lacking a large tooth, (0.2--0.4--0.6 mm long and (0.2--0.5--1(--1.3) mm wide (the smaller ones with 3 or even only 2 lobes); lobes all broadly ovate and acute, less than twice as long as wide, abaxially concave but the upper margins incurved towards the stem; cells somewhat elongated subbasally, (13--18--25(--30) x (12--15--20(--23) μm , those of lobes +/- quadrate, surface smooth or verruculose, cell walls with trigones rarely bulging; oil bodies 2--4 per cell. **Underleaves** transversely inserted and contiguous, symmetrical, 2-fid, and with much narrower lobes. **Androecia bracts** similar to leaves and with transitional forms, antheridial stalk 1- or 2-seriate, jacket cells not tiered. **Perianths** when fully developed longer than 1.5 mm. **Sporophytes** rare. **Seta** about 10 mm, cross section with one layer of quadrate cells, homogeneous interior ca. 10 cells across. **Capsule** 1.2 x 1 mm. **Elaters** worm-like, about 120 x 10 μm , brown. **Spores** 15--18 μm , finely spinulose.

Capsules mature in summer. Mountain slopes in Arctic or alpine tundra and in boreal forests, scrubs or dwarf shrub heaths, rarely on ground and not often in wet places, predominantly in exposed (rather than shaded) dry or mesic sites, preferred substratum a thin soil layer of mineral material and humus on siliceous rock outcrops or boulders, often admixed with *Racomitrium lanuginosum*, various lichens, ten different species of *Lophozia*, four different *Anastrophyllum*

species, *Ptilidium ciliare*, *Dicranum* sp., *Andreaea* sp. *Gymnomitrium* sp., and occasionally together with *Tetralophozia filiformis*; low to high elevations (0--2000 m); Greenland; Alta., B.C., Nfld., Nun., N.W.T., Ont., Que., Yukon; Alaska, Maine, N.H., N.Y., Vt.; Arctic; Europe; Asia.

Tetralophozia setiformis is a variable species, some of its modifications being very different from the more common form. The basal cilia often end in slime papillae. Sporophytes are extremely rare. I am aware of one single collection with young sporophytes from America (Steere 62-956). The above description is therefore based on European material I found fertile just once and with ripe capsules in Scandinavia. "*Tetralophozia setiformis* var. *alpina*", e.g., is very slender with small 3- or even 2-fid leaves. It occurs (with transition forms) within pure stands of normally grown plants or as whole populations under unfavourable conditions. I consider them in accord with Schuster (1966--1992, vol. 2, p. 251 f.) as mere modifications.

2. PLICANTHUS R.M. Schuster, Nova Hedwigia 74: 484. 2002 * [Latin/greek *plica* fold, *anthos* flower, alluding to the plicate perianth]

E. Urmi

Plants rather robust, but fragile when dry. **Stems** in cross section with firm-walled cells throughout; sometimes with paraphyllia. **Lateral leaves** squarrose and uneven, very deeply and asymmetrically 3-fid; lobes abaxially concave, acuminate, and +/- spiny; cells with very coarse trigones and occasionally with intermediate thickenings. **Underleaves** symmetrically 2-fid and little smaller than lateral leaves. **Asexual reproduction** lacking. **Sexual condition** dioicous. **Androecia** narrower than vegetative parts. **Gynoecia**: perianth strongly 6- to 8-plicate, mouth not tightly closed and longly ciliate. **Sporophytes** not observed in the flora.

Species 5 (1 in the flora); North America, Asia, Africa, Indian Ocean Islands, Pacific Islands, Australia.

SELECTED REFERENCES: Schuster, R. M. 2002. Revisionary studies of the Chandonanthoideae (Jungermanniales, Jungermanniaceae). Nova Hedw. 74: 465--496.

1. **Plicanthus hirtellus** (F. Weber) R. M. Schuster, Nova Hedwigia 74: 492. 2002

Jungermannia hirtella F. Weber, Hist. Musc. Hep. Prodr. 50. 1815; *Chandonanthus hirtellus* (F. Weber) Mitten in B. C. Seemann

Plants 30--70(--100) x (0.4--1.6--2.8(--4) mm, simple or sparingly branched, ascending in loose mats, yellowish green or ocher. **Stems** mostly 300 / μ m wide, but from 100 to 400 / μ m, branching terminal of *Frullania* type (except for innovations); cells in transverse section firm-walled throughout, gradually increasing in size from epidermis to the center; no paraphyllia seen, sometimes slime papillae in the axils of lateral leaves; rhizoids if any, in loose groups closely below underleaves, hyaline, ca. 11 / μ m wide. **Lateral leaves** succubous with oblique insertion, overlapping, hardly different when dry and wet, squarrose and very uneven, irregularly quadrangular in outline, very deeply and asymmetrically 3-fid with the sinuses abaxially

protruding, (0.2--1.8(--2) x (0.4--1.2--2.2(--3) mm, antical base often with a small secondary lobe, this and some basal cilia often ending in slime papillae; lobes unequal, the antical largest, all +/- ovate with acuminate apex, abaxially concave, median lobe about 30--40 cells wide at base, margins with many spines of various length, the largest lobe often less spinose; cells somewhat elongated, the subbasal ones (20--22--38(--41) x (10--13--20(--22) /um, surface verruculose, cell walls with coarsely nodulose trigones and intermediate thickenings in the longer cells; oil bodies 2--4 per cell, +/- spherical, botryoidal. **Underleaves** transversely inserted and contiguous, otherwise like the lateral leaves (including the cells), but somewhat smaller, symmetrical, and 2-fid. **Specialized asexual reproduction** unknown. **Sexual condition** dioicous. [**Androecia** intercalary, less wide than vegetative parts (1--1.5 mm), length and number of bracts indefinite, bracts smaller than lateral leaves, saccate, sometimes with paraphyses, bracteoles without antheridia.] **Gynoeceia** terminal on long shoots, innovations usually 1--2; bracts +/- 4, free and more crowded than leaves of vegetative parts, similar to these, but somewhat larger and 4-lobed; bracteoles 2, similar to underleaves; fully grown perianths (only young ones seen in North American specimens) exceeding the bracts, 3--4 mm, +/- fusiform, some antically curved, 6- to 8-plicate, mouth not tightly closed, somewhat lobed, and with several-celled cilia; ca. 15 archegonia in the perianth. **Sporophytes** unknown.

Humus under shrubs, cedar forest, dryer places of bogs or rock shelves; mostly with *Herbertus* sp.; low to moderate elevations; B.C.; Mexico; Asia, Africa, Indian Ocean Islands, Pacific Islands, Australia.

Plicanthus hirtellus is a rare species in North America confined to westernmost maritime Canada. The few known British Columbia populations are in the most northern stations worldwide.

3. BARBILOPHOZIA Loeske, Verh. Bot. Vereins Prov. Brandenburg 49(1): 37. 1907 * [Greek *barbil*, bearded, alluding to cilia on the leaves, and *lophos*, crest, spike, alluding to the angular ends of leaf lobes]

Terry T. McIntosh
Richard H. Zander
Alexey D. Potemkin

Neorthocaulis L. Söderström, De Roo & Hedderson; *Schljakovia* Konstant & Vilnet;
Schljakovianthus Konstant & Vilnet

Plants small to medium-sized, in loose to dense turfs or mats, prostrate, ascending, sub-erect, or erect, green, yellow-green, grayish-green, or dark brown, sometimes with a reddish or purple color. **Stems** branching terminal or lateral intercalary or occasionally both, transverse section with cortex 1--2(--3)-stratose; rhizoids sparse to common, colorless or pigmented proximally. **Leaves** succubous, obliquely, sometimes nearly transversely, inserted, distant to imbricate, spreading to appressed, flat to concave, obtrapezoidal, sub-orbicular, sub-quadrate or sub-rectangular, reniform, obtusate-quadrate, rarely nearly symmetric, divided by variously shaped sinuses into 2--4 lobes; lobes entire or, sometimes lightly toothed; lobes entire or sometimes apiculate or mucronate; sinuses of various lengths, gibbous or not; central laminal cells usually thin-walled and often trigonous, rarely papillose; oil bodies 2--25 per cell, biconcentric or not.

Underleaves usually present, usually 2-lobed, margins often ciliate. **Specialized asexual reproduction** by gemmae at apices of leaf-lobes or shoots, or absent; gemmae 1--2-celled, smooth or angular. **Sexual condition** dioicous. **Androecia** intercalary, 1--4-androus, antheridial stalk 1--2-seriate. **Gynoecea** terminal, female bracts in 1 pair, usually 3--6-lobed. **Perianth** cylindrical, mouth somewhat lobed and usually dentate or dentate ciliate, weakly to strongly plicate; perigynium absent. **Capsule** ovoid, walls 3--5-stratose, exterior wall with nodular thickenings, interior wall with semi-annular U-shaped thickenings, reddish brown. **Elaters** 2-spiraled, reddish brown. **Spores** spheric, 10--18 μm , papillose, brown.

Species 14 (12 in the flora): North America, South America, Eurasia, Africa, Australia, Oceania, Antarctica.

Barbilophozia and *Anastrophyllum* are both here recognized in Scapaniaceae. Both genera were moved to a new family *Anastrophyllaceae* L. Söderström, De Roo & Hedderson (L. Söderström et al. 2010), which was distinguished in part with molecular traits. They pointed out, however, that “the morphological characters that single out the family are not yet clear.” They also proposed the genus *Neoorthocaulis* L. Söderström, De Roo & Hedderson for four species of *Barbilophozia* largely based on molecular evidence. New genera, *Schljiakovia* Konstantinova & Vilnet and *Schljiakovianthus* Konstantinova & Vilnet, which included species of *Barbilophozia*, were also published by N. A. Konstantinova and A. A. Vilnet (2009) on a molecular basis. These classifications are here considered presently impractical, and a classical approach is adopted.

Diminutive plants of *Barbilophozia* are often difficult or impossible to separate from some species of *Lophozia*.

SELECTED REFERENCES Hong W. S. 2002. The distribution of *Lophozia* in North America west of the hundredth meridian. *Lindbergia*. 27: 49--62. Konstantinova, N. A. and A. A. Vilnet. 2009 [2010]. New taxa and new combinations in Jungermanniales (Hepaticae). *Arctoa* 18: 65--67. Schuster R. M. 1969. *Lophozia* (Dumort.) Dumort. In: R. M. Schuster. 1969. Hepaticae and Anthocerotae of North America. New York and London. Vol. 2. Schuster, R. M. and K. Damsholt. 1987. 1. New taxa from South Greenland. *Phytologia* 63(5): 325--328. Söderström, L., R. De Roo and T. Hedderson. 2010. Taxonomic novelties resulting from recent reclassification of the Lophoziaceae/Scapaniaceae clade. *Phytotaxa* 3: 47--53. Stotler, R. E. and B. Crandall-Stotler. 2017. A synopsis of the liverwort flora of North America north of Mexico. *Annals Missouri Bot. Gard.* 102: 574--709.

1. Lateral leaves mostly 2-lobed.

2. Lateral leaves evenly concave and nearly hemispheric, lobes not gibbous; underleaves usually absent, if present minute..... 5. *Barbilophozia cavifolia*

2. Lateral leaves never evenly concave nor hemispheric; lobes +/- gibbous; underleaves present and distinct, lanceolate or 2-lobed.

3. Plants small, ca. 0.3--0.6 mm wide, blackish to olive-brown; leaves subtransversely inserted; laminal cells usually coarsely papillose with large, low papillae; Arctic 11. *Barbilophozia quadriloba* (in part)

3. Plants larger, ca. 0.6--1 mm wide, green and yellow brown to brown-fuscous; leaves mostly obliquely inserted; laminal cells lacking large, low papillae.

4. Plants light green and yellow brown; leaves with broadly ovate to triangular \pm concave to plane lobes; oil bodies (1--2--4(--5) per cell; Arcto-boreal-montane 9. *Barbilophozia kunzeana* (in part)
4. Plants green to brown and brown-fuscous; Leaves with broadly triangular acute \pm concave lobes; oil bodies (4--7--15 per cell; Arctic only..... 8. *Barbilophozia hyperborea* (in part)
1. Lateral leaves mostly (2--3--4-lobed.
5. Lateral leaves subtransversely inserted and oriented, deeply lobed with sinuses $2/5$ -- $3/5$ leaf length, lobes usually 4, but some plants strictly 3-lobed; laminal cells coarsely papillose with numerous large, low papillae 11. *Barbilophozia quadriloba* (in part)
5. Lateral leaves obliquely inserted and oriented, more shallowly lobed with sinuses $1/5$ - $2/5$ leaf length or less, lobes usually 3 or 4; laminal cells never coarsely papillose.
6. Leaves mostly (3--4-lobed.
7. Lateral leaves only slightly narrowed to the base, nearly symmetric, lying almost parallel to stem; lobes obtuse to subacute and never mucronate at apex, subequal in size, lateral slightly smaller than median; postical leaf bases unarmed; underleaves absent or minute 3. *Barbilophozia barbata*
7. Lateral leaves distinctly narrowed to base, not symmetric, not lying parallel to stem; lobes often mucronate at apex, unequal in size; postical leaf bases with 1-several cilia; underleaves present.
8. Plants often red pigmented (purple or carmine) at shoot apices, leaf bases, and underleaves; central laminal cells 30--40 μm wide; oil-bodies up to 26--28 per cell; underleaves small and indistinct; Greenland..... 12. *Barbilophozia rubescens*
8. Plants lacking red pigments; central laminal cells 16--28 μm wide; oil-bodies 2--10 per cell; underleaves large and distinct; widespread.
9. Plants up to 4--4.5(--5) mm wide; leaves usually +/- undulate; apices of leaf lobes mostly with spinose mucros; postical leaf bases often composed of long and often numerous cilia of strongly elongated cells; gemmae usually absent10. *Barbilophozia lycopodioides*
- 9..Plants (0.5--1.5--2(--3.3) mm wide; leaves not or slightly undulate; apices of leaf lobes usually acute to mucronate; postical leaf bases composed of few cilia of moderately elongated cells; gemmae usually present, abundant. 7. *Barbilophozia hatcheri*
6. Lateral leaves mostly (2--3-lobed.
10. Underleaves absent or minute, well under $1/5$ leaf length.
11. Attenuate, erect gemmiferous shoots with closely appressed leaves with reduced lobes usually present, filiform; laminal cells with usually small and concave-sided trigones; gemmae mostly pale green, in exposed sites partly reddish or vinaceous. 2. *Barbilophozia attenuata*

11. Attenuate, erect gemmiferous shoots absent or present and not filiform; laminal cells often with large, convex-sided trigones. Gemmae sporadically present, red or purplish red.
12. Plants erect or suberect usually growing among mosses, rarely on rock; underleaves absent; mature leaves invariably 3-lobed with sinuses $1/4$ -- $1/2$ the leaf length.
..... 4. *Barbilophozia bistedii*
12. Plants procumbent and slightly ascending to suberect, usually growing on rocks, occasionally on soil and among mosses; underleaves absent or small and filiform to oblong and bi-lobed; mature leaves 2--3(--4)-lobed, with sinuses 0.25 -- 0.4 the leaf length. .1. *Barbilophozia atlantica*
10. Underleaves large, up to $1/2$ leaf length or longer.
13. Underleaves usually about or less than half the leaf length.
..... 9. *Barbilophozia kunzeana* (in part)
13. Underleaves more than half the leaf length.
14. Plants usually large to robust, (1--) 1.8 -- 3 (-- 5) wide; sinuses $1/8$ -- $2/5$ leaf length; gemmae absent.
..... 6. *Barbilophozia floerkei*
14. Plants medium-sized, 0.8 -- 1.1 mm wide; sinuses $1/3$ -- $1/2$ leaf length; gemmae present or absent 8. *Barbilophozia hyperborea* (in part)

1. *Barbilophozia atlantica* (Kaalaas) Müller Frib , Leberm. Eur., 639. 1954

Jungermannia atlantica Kaalaas, Skr. Vidensk.-Selsk. Christiania, Math.-Naturvidensk. Kl. 1898(9): 11. 1898; *Orthocaulis atlanticus* (Kaalaas) H. Buch

Plants 1--3(--5) cm x 0.4 -- 0.8 (--2) mm, prostrate to ascending, rarely erect, usually in mats, sometimes in cushions, green, yellow-green to dark gray-green, or yellow-brown or brownish red, sometimes with a purple tinge. **Stems** with shoots sometimes weakly attenuate and gemmiferous. **Lateral leaves** weakly obliquely inserted, erecto-patent or patent, not secund, sub-orbicular to obtrapezoidal, usually complicate-concave, occasionally more or less horizontal and partly convex, not or slightly undulate, 0.6 -- 1.2 (-- 1.5) x 0.4 -- 0.8 (--1) mm, unequally (2--) 3 (--4)-lobed, apices acute to sub-acute, rarely rounded, margins often irregularly slightly sinuous or erose on older leaves, rarely apiculate distally, postical base unarmed or with a small tooth, slime papilla, or short-celled cilium; sinuses $1/8$ -- $2/5$ leaf length, usually gibbous; central laminal cells 4--5 angular, 20 -- 23 x 28 -- 30 μm , walls thin, trigones large and convex, sometimes concave-sided, oil bodies (3--) 5 -- 7 (-- 10) per cell. **Underleaves** absent or small and filiform to oblong and bi-lobed. **Specialized asexual reproduction** as sub-orbicular or angular gemmae usually present on non-modified or weakly, erect attenuate shoots, gemmae red or purplish red, 18 -- 28 x 20 -- 42 (-- 56) μm , 1--2-celled. **Sexual condition** dioicous. **Gynoecea** more frequent, bracts 2--5 lobed, bracteole 2--3 lobed. **Perianth** mouth dentate or dentate-ciliate; mature perianths unknown.

Exposed to shaded, often calcareous rock, often in crevices, occasionally on soil and among mosses; arctic-alpine; 0--1000 m; Greenland; Nfld. and Labrador (Labr.), Nun., Ont., Que; Maine, N.H; Eurasia.

Traits characteristic of *Barbilophozia atlantica* are the arctic-alpine range, sometimes weakly attenuate gemmiferous shoots, red to purple gemmae, and large leaf cells usually with bulging trigones.

2. *Barbilophozia attenuata* (Martius) Loeske, Verh. Bot. Vereins Prov. Brandenburg 49: 37. 1907

Jungermannia attenuata fo. *attenuata* Martius, Fl. Crypt. Erlang., 177. 1817; *Neoorthocaulis attenuata* (Martius) L. Söderström, De Roo & Hedderston; *Orthocaulis attenuata* (Martius) A. Evans

Plants 1--3 (--5) cm x 0.7--1.8 mm, prostrate to sub-erect, in mats, green or yellow-green, sometimes brownish or with a red tinge. **Stems** commonly developing filiform, innovations from shoot apices. **Lateral leaves** somewhat obliquely inserted, spreading, sub-quadrate or obtrapezoidal, 0.7--0.9 x 0.7--0.8(--1) mm, (2--3)--(3--4)-lobed, lobes concave or straight-sided, apices acute to sub-acute, sometimes apiculate, postical base unarmed, sinuses 1/3--1/4 leaf length, rarely weakly gibbous; central laminal cells 4--5 angular, 15--20 x 15--25 μm , walls thin or slightly thickened, trigones absent or small, sometimes large, usually concave, oil bodies (3--6)--10 per cell. **Underleaves** absent or represented by small cilium. **Specialized asexual reproduction** as polymorphous gemmae on filiform, often erect innovations bearing imbricate, weakly tri-lobate leaves, gemmae green, sometimes orange or weakly vinaceous in exposed sites; 18--22 x 22--35 μm , 1--2-celled. **Sexual condition** dioicous. **Gynoecea** with bracts 3--5 lobed, bracteole 2--4 lobed. **Perianth** cylindrical or oblong-cylindrical, plicate, mouth lacinate and ciliate.

Boulders and ledges, talus and rocky slopes, decaying wood; 0--2000 m; Greenland; Alta., B.C., N.B., Nfld. and Labr. (Nfld., Labr.), N.S., Nun., Ont., Que.; Alaska, Colo., Conn., Idaho, Maine, Mass., Mich., Minn., Mont., N.H., N.Y., N.C., Penn., Tenn., Vt., Va., Wash., W.Va., Wis., Wyo.; Eurasia; Atlantic Islands (Azores).

Barbilophozia attenuata commonly has attenuate gemmiferous shoots as does *B. atlantica* but the attenuation is abrupt and narrow, not gradual and indistinct as in the latter species. Additional distinctive traits are the relative lack of postical cilia and the small laminal cells of *B. attenuata*.

3. *Barbilophozia barbata* (Schmidel ex Schreber) Loeske, Verh. Bot. Vereins Prov. Brandenburg 49: 37. 1907 F

Jungermannia barbata Schmidel ex Schreber, Spic. Fl. Lips., 107. 1771

Plants 3--8 cm x 2--5 mm, prostrate, sometimes ascending distally, in loose mats, dark green or green, sometimes brownish green, rarely brown. **Stems** without distinctive innovations. **Lateral leaves** obliquely inserted, wide-spreading, obtusely-quadrate and nearly symmetric, usually lying almost parallel to stem, only slightly narrowed to the base, up to (0.8--1)--1.8(--1) mm, (3--4)-lobed, lobes +/-triangular, sub-equal in size with lateral ones slightly smaller, slightly

concave, or straight-sided, apices obtuse to sub-acute, not mucronate, postical base unarmed, sinuses 1/6--1/4 leaf length, not or slightly gibbous; central laminal cells rounded-polygonal, 20--25 x 23--30 μm , walls thin, trigones absent or small and concave, oil bodies 4--9(--12) per cell. **Underleaves** absent or minute, subulate or lanceolate, usually 2-fid. **Specialized asexual reproduction** rare as reddish-yellow, angulate gemmae, 1--2-celled. **Sexual condition** dioicous. **Gynoecia** with bracts 3--5 lobed, bracteole 2--4 lobed. **Perianth** oblong-cylindrical, deeply plicate, mouth crenulate or dentate. **Capsule** wall 4-stratose.

Cliffs and outcrops, crevices and ledges, loamy or rocky banks, humus, peaty depressions; 0--1000 m; Greenland; Miquelon; Alta., B.C., N.B., Nfld. and Labr. (Nfld.), N.S., N.W.T., Nun., Ont., Que., Sask., Yukon; Alaska, Ariz., Colo., Conn., Idaho, Ind., Maine, Mass., Mich., Minn., Mont., N.H., N.M., N.Y., N.C., Penn., Vt., Va., Wash., Wis., Wyo.; Eurasia; Atlantic Islands (Iceland).

The nearly quadrate leaves lying almost parallel to stem make *Barbilophozia barbata* the most easily recognized species in the genus. The triangular leaf lobes lack terminal mucros, and the underleaves are absent or very small.

4. *Barbilophozia binsteadii* (Kaalaas) Loeske, Hedwigia 49: 13. 1909

Jungermannia binsteadii Kaalaas, Skr. Vidensk.-Selsk. Christiana, Math.-Naturvidensk. Kl. 1898(9): 9. 1898; *Lophozia binsteadii* (Kaalaas) A. Evans; *Neoorthocaulis binsteadii* (Kaalaas) L. Söderström, De Roo & Hedderson

Plants 1--3 cm x 0.5--1.2 mm, erect or suberect usually among mosses, often crowded and more or less caespitose, golden-brown to chestnut brown. **Stems** without distinctive innovations, seldom with gemmiferous shoots. **Lateral leaves** obliquely inserted, sub-erect and concave (cup-like), sub-quadrate or narrowly obtrapezoidal, usually imbricate and dorsally more or less secund, 0.6--0.9(--1.1) x 0.7--0.95 mm, (2--3)-lobed, lobes sub-equal in shape, apices acute, postical base unarmed, sinuses 1/4--1/2 leaf length, usually weakly gibbous; central laminal cells rounded-polygonal, 17--23 x (18--24--30) μm , walls thin or slightly thickened, trigones large, convex, oil bodies mostly 3--6 per cell. **Underleaves** absent or reduced to slime papillae. **Specialized asexual reproduction** rare, as vinaceous red or deep metallic purple, angulate gemmae, 1--2-celled. **Sexual condition** dioicous. **Gynoecia** with bracts similar to lateral leaves but 3--5 lobed, bracteole large and 2-lobed. **Perianth** cylindrical-clavate, deeply plicate, mouth with small, ciliate-dentate lobes.

Tundra, bogs, peaty depressions, rarely on shaded rock, strongly associated with *Sphagnum* spp. and *Calypogeia sphagnicola*; arctic-alpine; 0--2000 m; Greenland; Alta., B.C., N.B., Nfld. and Labr. (Labr.), N.S., Nun., Que., N.W.T., Yukon; Alaska; n Eurasia.

Barbilophozia binsteadii is distinguished by its mostly erect plants usually among mosses, the usually 3-lobed, rather cupped leaves with narrow, deep sinuses and narrow lobes, and leaf cells with large trigones. Underleaves are absent.

5. *Barbilophozia cavifolia* (H. Buch & S. Arnell) Stotler & Crandall-Stotler, Bryologist 80: 426. 1977

Orthocaulis cavifolius H. Buch & S. W. Arnell, Memoranda Soc. Fauna Fl. Fen. 26: 71. 1951; *Anastrophyllum cavifolium* (H. Buch & S.W. Arnell) Lammes; *Lophozia cavifolia* (H. Buch & S. W. Arnell) R. M. Schuster

Plants 1--3 cm x 0.7--1.1 mm, erect or suberect among mosses, brown to reddish-brown, green in shaded sites. **Stems** without distinctive innovations. **Lateral leaves** almost transversely inserted, widely spreading, more or less hemispheric, usually remote to contiguous and antically more or less secund, strongly concave, 0.65--0.9 x 0.5--0.95(--1.2) mm, 2(--3 rarely 4) lobed, lobes sub-equal in shape, apices obtuse, incurved, postical base unarmed, sinuses 1/3--1/4 leaf length, not gibbous; central laminal cells mostly 4-sided and isodiametric or short-rectangular, 22--28 x 25--35(--40) μ m, walls thin or slightly thickened, trigones large, usually convex, oil bodies (2--6--8(--12) per cell. **Underleaves** usually absent or minute, linear-subulate or linear-lanceolate, usually 2-lobed. **Specialized asexual reproduction** sparse as reddish brown, angulate gemmae, (1--2)-celled. **Sexual condition** dioicous. **Gynoecia** unknown.

Tundra, peatlands, amongst other mosses; Arctic; 0--200 m; Greenland; Eurasia.

Barbilophozia cavifolia is characterized by mostly 2-lobed leaves that are strongly concave and nearly hemispheric, with laminal cells usually having large, convex-sided trigones. This species resembles robust *Sphenolobus minutus* from which it is distinguished by (4--5)6--8(--12) oil bodies per cell.

6. Barbilophozia floerkei (Weber & D. Mohr) Loeske, Verh. Bot. Vereins Prov. Brandenburg 49: 37. 1907

Jungermannia floerkei F. Weber & D. Mohr. Bot. Taschenb., 410. 1807; *Orthocaulis floerkei* (F. Weber & D. Mohr) H. Buch

Plants 2--5(--10) cm x (1--1.8--3(--5) mm, prostrate, suberect, or erect, in mats, often intertwined with mosses, pale or yellow-green to dark green, sometimes brownish green. **Stems** without distinctive innovations. **Lateral leaves** obliquely inserted, patent, spreading, or subsquarrose, subquadrate to sub-rectangular, nearly orbicular, or obtrapezoidal, imbricate, concave or convex, sometimes undulate, (0.5--0.9--2 x (0.5--1--1.5) mm, (2--3(--4)-lobed, lobes sub-equal in size, apices obtuse to broadly-acute, postical base with 1--3(--6) relatively short cilia composed of +/-isodiametric cells, sinuses 1/8--2/5 leaf length, weakly to strongly gibbous; central laminal cells more or less rounded-polygonal, 16--20 x 20--26 μ m, walls thin, trigones large and slightly convex to minute, oil bodies 2--6(--7) per cell. **Underleaves** large, 2-fid and divided to near base, short-ciliate near base, lobes lanceolate-acuminate and usually ending in a short cilium. **Specialized asexual reproduction** absent. **Sexual Condition** dioicous. **Gynoecia** with bracts 3--4(--7) lobed, bracteole 2-lobed. **Perianth** ovate-cylindrical, deeply plicate, mouth ciliolate or dentate.

On humus, boulders; 0--2000(--3100) m; Alta., B.C., Nfld. and Labr. (Nfld.), N.S., N.W.T., Nun., Que., Yukon; Alaska, Colo., Maine, Mont., N.H., N.Mex., Vt., Wash., Yukon; South America (Peru); n. Europe.

Barbilophozia floerkei usually has subquadrate to sub-rectangular leaves with short cilia on postical margins, composed of near isodiametric cells, and the underleaves are relatively large. It lacks gemmae.

7. *Barbilophozia hatcheri* (A. Evans) Loeske, Verh. Bot. Vereins Prov. Brandenburg 49: 37. 1907

Jungermannia hatcheri A. Evans, Bull. Torrey Bot. Club 25: 417. 1898

Plants 2--5 cm x 1--2(--3) mm, prostrate, suberect, or erect, in patches or mats, green or brown, sometimes brownish green. **Stems** without distinctive innovations. **Lateral leaves** obliquely inserted, patent or spreading, shape variable, mostly obtrapezoidal, approximate or imbricate, more or less flat, 1--1.5(--2) x 1--1.3 mm, (3--4)-lobed, lobes sub-equal in size with lateral ones smaller, apices acute or obtuse, usually with distal apiculus, rarely with short mucros, postical base with 2--3(--6) relatively short cilia usually composed of elongate-rectangular cells, sinuses 1/5--2/5 leaf length, gibbous or not; central laminal cells quadrate or hexagonal, 20--26 x 18--25 μ m, walls thin, trigones small to medium-sized, slightly convex, oil bodies 2--5(--10) per cell. **Underleaves** large, usually 2-fid and divided to near base, or lanceolate, 10--16 cells wide proximally, long-ciliate at base, cilia often contorted, lobes lanceolate-acuminate, usually ending in a long cilium. **Specialized asexual reproduction** usually abundant as reddish brown, angulate gemmae, 2-celled. **Sexual condition** dioicous. **Gynoecea** with bracts 3--5-lobed, bracteole 2 or 3-lobed. **Perianth** ovoid-cylindrical, plicate, mouth short-dentate or short-ciliolate.

On cliffs, ledges, acidic or somewhat basic rock, particularly under spruce and fir; 300--3000 m elv.; Greenland; Alta., B.C., Nfld. and Labr. (Nfld. and Labr.), N.S., Nun., Ont., Que., Yukon; Alaska, Calif., Colo., Idaho, Maine, Mich., Minn., Mont., N.H., N.Y., N.C., Oreg., Tenn., Utah, Wash., Wyo.; South America (s Argentina); Atlantic Islands (Falklands); Eurasia; Antarctica.

Barbilophozia hatcheri is bipolar in distribution and the only species of the genus to occur in Antarctica. The leaves are usually 4-lobed and obliquely inserted. The leaf lobes are usually apiculate, and the postical bases have short cilia composed of elongate cells. The underleaves are large and bear cilia. This species is often confused with smaller plants of *B. lycopodioides*. It is also similar to *B. rubescens*. See comparative notes under those species.

8. *Barbilophozia hyperborea* (R. M. Schuster) Stotler & Crandall-Stotler ex Potemkin, Novosti Sist. Nizsh. Rast. 28: 148. 1992

Lophozia floerkei var. *hyperborea* R. M. Schuster, Bull. Natl. Mus. Canada 164: 21. 1959; *L. hyperborea* (R. M. Schuster) R. M. Schuster; *L. hyperborea* ssp. *helophila* R. M. Schuster; *Neorthocaulis hyperboreus* (R. M. Schuster) L. Söderström, De Roos & Hedderon; *Orthocaulis hyperboreus* (R. M. Schuster) Konstantinova, Novosti Sist. Nizsh. Rast. 30: 112. 1995

Plants 1--2 cm x 0.8--1.1 mm, patent or suberect among other bryophytes, brown to brownish-black, sometimes with a red cast. **Stems** without distinctive innovations. **Lateral leaves** obliquely inserted, erect or sub-erect, oblong or obtrapezoidal, patent and imbricate, concave to concave-folded, 0.4--1 x 0.4--0.8 mm, (2--3)(rarely 4)-lobed, lobes sub-equal in size, often longer than wide, incurved, apices usually acute, sometimes obtuse, sometimes with distal

apiculus, postical base with 1--3 short teeth, less often with short cilia, sinuses 1/3--1/2 leaf length, weakly to strongly gibbous; central laminal cells usually rounded-polygonal, 20--26 x 20--28(--30) μm , walls thin, with coarse cuticles, trigones small to medium-sized, usually concave, oil bodies (4--7)--15 per cell. **Underleaves** large, rarely small to minute, 2-fid and divided to near base, toothed, sometimes ciliate or laciniate at base, lobes lanceolate-acuminate, usually ending in a long cilium. **Specialized asexual reproduction** absent or present. **Sexual condition** dioicous. **Gynoecea** with bracts 2--3-lobed, bracteole 2-lobed. **Perianth** ovoid, weakly plicate, mouth ciliate-dentate and lobulate-cililate.

Soil, rock; low elevations; Greenland; Nun.; Alaska.

Barbilophozia hyperborea is distinguished in part by brown coloration, leaves oblong or obtapezoidal, with 1--3 short teeth on postical bases, and laminal cells with a coarse cuticle and many oil bodies per cell, and large underleaves.

1. Plants without a red coloration, underleaves large, gemmae absent
8a. *Barbilophozia hyperborea* subsp. *hyperborea*
1. Plants with a red coloration, underleaves small to minute, gemmae present
8b. *Barbilophozia hyperborea* subsp. *helophila*

8a. Barbilophozia hyperborea subsp. **hyperborea**

Plants without a red coloration. **Underleaves** usually large. **Specialized asexual reproduction** absent.

Wet sites, soil and shale below snow banks and fen-ice cliffs; moderate elevations; Greenland; Nun. (Ellesmere I.); Alaska; n Eurasia.

Specimens of *Barbilophozia hyperborea* fo. *paradoxa* R. M. Schuster, known from northern Greenland, apparently differ in having only 2--7 oil bodies per cell, coarse trigones, and nearly smooth laminal cell cuticle.

8b. Barbilophozia hyperborea subsp. **helophila** (R. M. Schuster & Damsholt) R. H. Zander, *Phytoneuron* 2020-17: 1. 2020. E

Lophozia hyperborea ssp. *helophila* R. M. Schuster & Damsholt, *Phytologia* 63: 325. 1987;
Neorthocaulis hyperboreus subsp. *helophilus* (R. M. Schuster & Damsholt) Stotler & Crandall-Stotler

Plants with a red coloration. **Underleaves** small to minute. **Specialized asexual reproduction** by gemmae.

Wet sites, soil and rock; low to moderate elevations; s Greenland.

Barbilophozia hyperborea subsp. *helophila* is restricted to southern Greenland, and was distinguished by R. M. Schuster and K. Damsholt (1987) from the typical subspecies by the key traits above.

SELECTED REFERENCE Zander, R.H. 2020. A new combination in *Barbilophozia* for *Lophozia hyperborea* subsp. *helophila* (Scapaniaceae, Marchantiophyta) of Greenland, with macroevolutionary justification. *Phytoneuron* 2020-17: 1–3.

9. *Barbilophozia kunzeana* (Hübener) Müll. Frib., Mitteil. Badischen Landesver. Naturk. Naturschutz, N. F. 4: 431. 1944
Jungermannia kunzeana Huebener, Hepaticol. Germ., 115. 1834; *Lophozia kunzeana* (Huebener) A. Evans; *Orthocaulis kunzeanus* (Huebener) H. Buch; *Schljakovia kunzeana* (Huebener) Konstantinova & Vilnet

Plants 2--5(--8) cm x 0.6--1.5 mm, erect or ascending, solitary or in patches, often intertwined with mosses, yellow-brown to chestnut brown, sometimes bright green. **Stems** without distinctive innovations. **Lateral leaves** obliquely to nearly transversely inserted especially distally, patent or spreading, sometimes upper portions nearly erect, sub-quadrate to nearly orbicular, approximate to sub-imbricate, concave or convex, 0.6--0.8(--1) x 0.6--0.9(1.2) mm, 2(- - rarely 3)-lobed, lobes sub-equal in size, apices obtuse to rounded, occasionally acute, rarely apiculate, usually incurved, postical base usually unarmed, rarely with a short cilium or tooth, sinuses (1/6--)1/4 – 1/2 leaf length, gibbous; central laminal cells more or less isodiametric, less often short-rectangular, rounded-polygonal, 17--20 x 21--26 μ m, walls thin, trigones small, concave, rarely convex, oil bodies (1--)2--4(--5) per cell. **Underleaves** small, 2-fid and divided to near base, sometimes undivided, lobes lanceolate, sometimes with 1(--3) basal teeth. **Specialized asexual reproduction** uncommon, yellow-green, brown, or orange-brown angulate gemmae, 1--2-celled. **Sexual condition** dioicous. **Gynoecea** with bracts larger than lateral leaves, 3--4(--6) lobed, bracteole 2-lobed. **Perianth** oblong-ovoid, plicate, mouth dentate-serrate, teeth ciliate.

On wet peat over rock, soil, arctic-alpine, heath; 0--1500 m elev.; Greenland; B.C., N.W.T., Nun., Ont., .Sask., Que., Yukon; Alaska, Colo., Maine, Mich., Minn., N.H., N.Y.; Eurasia.

Females plants of *Barbilophozia kunzeana* are usually larger than male plants. The leaves lack postical cilia and are largely 2-lobed.

10. *Barbilophozia lycopodioides* (Wallroth) Loeske, Verh. Bot. Vereins Prov. Brandenburg 49: 37. 1907

Jungermannia lycopodioides Wallroth, Fl. Crypt. Germ. 1: 76. 1831

Plants 2--5(--10) cm x 1.5--3(--5) mm, prostrate, sometimes suberect, in mats, often intertwined with mosses, green, pale green, or stramineous yellow, rarely brownish. **Stems** without distinctive innovations. **Lateral leaves** obliquely inserted, spreading, obtuse, asymmetrical, imbricate, usually undulate, sometimes crispate, 2--3 x 1.5--2 mm, (rarely 3--)4-lobed, lobes sub-equal in size, apices obtuse, sometimes broadly acute, usually with 1--3 celled mucros, often longest on postical lobe, postical base with 4--7 long and slender cilia composed of elongate

cells, sinuses 1/10--1/4 leaf length, weakly to strongly gibbous; central laminal cells rounded-polygonal or short-rectangular, 20 x 25--28 μm , walls thin, trigones large and slightly convex to minute, oil bodies 2--5(--10) per cell. **Underleaves** large, 2-fid and divided to near base, rarely lanceolate, strongly ciliate, cilia (3--5)--7(--8) long and tortuous, lobes lanceolate-acuminate and ending in a long cilium. **Specialized asexual reproduction** rare as reddish-brown, angulate gemmae, 2-celled. **Sexual Condition** dioicous, usually sterile. **Gynoecia** with bracts 4--5 lobed, bracteole 2(--4)-lobed. **Perianth** ovate-cylindrical, plicate, mouth dentate. **Capsule** wall 3-stratose.

On well-drained humus, rock walls, ledges; 0--1500 m elv., Greenland; Alta., B.C., Nfld. & Labr. (Labr.), N.W.T., N.S., Que., Yukon; Alaska, Colo., Mont., N.Mex., Utah. Wash., Wyo.; Eurasia.

Barbilophozia lycopodioides has been confused with larger plants of *B. hatcheri*. The leaves of *B. lycopodioides*, however, are more shallowly lobed and the lobes broader and more strongly gibbous and are often tipped with a long mucro. Also, the antical leaf margins of *B. lycopodioides* across the mid-line of the stem, whereas those of *B. hatcheri* do not extend that far.

11. *Barbilophozia quadriloba* (Lindberg) Loeske, Hedwigia 49: 13. 1909

Jungermannia quadriloba Lindberg in Lindberg & Arnell, Kongl. Svenska Vetensk.-Akad. Handl. (n. ser.) 23: 55. 1889; *Lophozia quadriloba* (Lindberg) A. Evans; *Orthocaulis quadriloba* (Lindberg) A. Evans

Plants 0.6--2.5(--4) cm x 0.5--1.8 mm, erect, sometimes sub-erect or procumbent, in tufts or dense patches, fuscous or olive-green or brownish, sometimes with inky cast. **Stems** without distinctive innovations. **Lateral leaves** subtransversely inserted, spreading with lobes sub-erect or erect, obtuse, distant to contiguous, imbricate distally on stems, often concave and cupped, 1--1.5 x 0.5--1.3 mm, often wider than long, (rarely 2--3--4)(rarely--5)-lobed, lobes ovate-triangular, sub-equal in size, sometimes dorsal lobe larger, apices acute, postical base with 1--3 cilia or teeth, antical base less ornamented, with 1--3 teeth or short cilia, or not ornamented, sinuses 2/5--3/5 leaf length, often rounded and open near base on larger leaves, unevenly (wavy) gibbous; central laminal cells rounded-polygonal, 22--25(--35) x 18--24 μm , walls thin or slightly thickened, coarsely papillose with large, low papillae, trigones minute to large, rarely convex, oil bodies 4--9 per cell. **Underleaves** large, 2-fid and divided to near base, sometimes lanceolate and small, usually long- and short-ciliate at base, lobes linear-lanceolate, acuminate. **Specialized asexual reproduction** absent. **Sexual Condition** dioicous, usually sterile. **Gynoecia** with bracts 4--5 lobed, bracteole 2-lobed. **Perianth** oblong-obovoid, plicate, mouth lobulate-dentate.

The unique trait of large, low papillae on the laminal cell wall cuticles, except in highly reduced forms, is characteristic of *Barbilophozia quadriloba*. This species is also distinctive in the usually 4-lobed leaves with deep sinuses, although some smaller plants have only 2- or 3-lobed leaves, and gemmae are absent. The var. *glareosa*, a reduced variant with mostly 3-lobed leaves with lobes little reflexed, was recently reduced to *Barbilophozia quadriloba* fo. *glareosa* (E. Jørgensen) Potemkin and is not recognized in the Flora. Likewise, the var. *glareosa* fo.

cephalozielloides R. M. Schuster, an extremely reduced form of the variety, characterized by its 2-lobed lateral leaves, is not recognized. It resembles some species of *Cephaloziella* but is distinguished by its larger leaf cells and longer and lanceolate-lobed underleaves. Slender forms of *Chandonanthus setiformis* strongly resemble *B. quadriloba* but it is a warmer brown and clearly shiny when dry, and has dentate, more deeply divided leaf lobes.

On soil, humus; low to moderate elevations; Greenland; North America (Canada, n U.S.A.); Eurasia; Atlantic Islands.

1. Central leaf cells averaging 22--25 x 18--19 μm , with small, less distinct, rarely slightly convex trigones 11a. *Barbilophozia quadriloba* var. *quadriloba*
 1. Central leaf cells averaging 25--35 x 20--24 μm , with large and distinct, often convex trigones 11b. *Barbilophozia quadriloba* var. *collechymatica*

11a. *Barbilophozia quadriloba* (Lindberg) Loeske var. *quadriloba*

Barbilophozia quadriloba var. *glareosa* (E. Jørgensen) Lammes in T. Koponen, Isoviita & Lammes

Laminal cells averaging 22--25 x 18--19 μm , with small, less distinct, rarely slightly convex trigones.

On slopes below snow banks, thin soil or humus over basaltic or calcareous rock; 0--1300 m elv.; Greenland; B.C., Nfld. and Labr. (Nfld.); Nun., Ont.; Alaska, Mich.; Eurasia; Atlantic Islands (Iceland).

11b. *Barbilophozia quadriloba* var. *collechymatica* (R. M. Schuster) Stotler & Crand.-Statl.
 Bryologist 80: 410. 1977

Lophozia quadriloba (Lindb.) A. Evans var. *collechymatica* R. M. Schuster, Hepat. Anthocerotae N. Amer. 2: 81. 1969; *Schljakovianthus quadrilobus* var. *collechymaticus* Konstantinova & Vilnet, Arctoa 18: 66. 2009 [2010]

Laminal cells averaging 25--35 x 20--24 μm , with large and distinct, often convex trigones.

On soil, humus; low to moderate elevations, Greenland.

12. *Barbilophozia rubescens* (R. M. Schuster & Damsholt) Karttunen & L. Söderström, Ann. Bot. Fenn. 29: 120. 1992

Lophozia rubescens R. M. Schuster & Damsholt, Phytologia 63: 325. 1987; *Barbilophozia hatcheri* var. *grandiretis* H. Buch ex Lammes

Plants 2--4 cm x 2.5--3.5 mm, prostrate or ascending, in loose tufts and patches, yellowish green to light brown, shoot apices, leaf bases, and underleaves usually red pigmented (purple or carmine). **Stems** without distinctive innovations. **Lateral leaves** obliquely inserted, densely imbricate with lobes incurved, obtuse to reniform, concave, 1--1.5 x 1--1.3(--2) mm, 3(--4)-lobed, lobes triangular, sub-equal in size with lateral ones smaller, apices acute, sometimes obtuse, usually with distal mucro, sometimes short-ciliate, postical base with 4--6(--7) long,

contorted thread-like cilia usually composed of elongate-rectangular cells, sinuses 1/5--1/3(--1/2) leaf length, gibbous or not; central laminal cells quadrate to short-rectangular, (30--32--35(--38) x 35--42/um, walls thin, trigones weakly developed to scarcely bulging, oil bodies 5--28 per cell. **Underleaves** indistinct, 2-lobed and divided up to ca. 0.9 of length, 4--6 cells wide proximally, with cilia on margins near apex or almost throughout, lobes lanceolate, ending a long cilium. **Specialized asexual reproduction** by gemmae, vinaceous, angular, 1--2-celled, rare. **Sexual condition** dioicous. **Gynoecea** with bracts 2-lobed, bracteole 2-lobed. **Perianth** ovoid, plicate, mouth with scattered 1--3-celled teeth.

On wet acidic or calcareous soil; low elevations; s Greenland; n Europe.

As implied by its epithet, *Barbilophozia rubescens* is distinguished in part by the commonly intensely red shoot apices, leaf bases, and underleaves. The leaves are 3(--4)-lobed, underleaves are present but small, and gemmae few or absent. *Barbilophozia rubescens* is similar to densely leaved plants of *B. hatcheri*. The leaves, however, are more shallowly lobed and the lobes broader and more strongly gibbous.

EXCLUDED

Barbilopholia sudetica (Nees ex Huebener) L. Söderström, De Roo & Hedderson is in FNA treated as *Lophozia sudetica* (Nees ex Huebener) Grolle.

4. BIANATHERIDION (Grolle) Konstantinova & Vilnet, Arctoa 18: 67. 2009 [2010]

Jamesoniella sect. *Biantheridion* Grolle, Trans. Brit. Bryol. Soc. 4: 662. 1964

Marie L. Hicks

Plants prostrate to erect-caespitose when crowded, slightly laterally compressed, simple or with few branches, green to reddish-brown. **Stem** firm, cortex not differentiated; branches terminal. **Leaves** succubous, not especially soft, symmetrical, plane or undulate, unlobed, rounded or shallowly retuse, entire, upper base decurrent, lower base not decurrent; cell walls slightly thickened; trigones present, occasionally slightly bulging, marginal cells similar. **Underleaves** very small and sporadic on sterile shoots or absent. **Specialized asexual reproduction** absent. **Gynoeceal** bracts closely enveloping base of perianth; perianth persistent, oblong-ovoid, distally plicate, narrowed to mouth.

Species 1 (1 species in the flora): Greenland, Europe, Asia.

The single species of *Biantheridion* has often been included in *Jamesoniella* (a synonym of *Syzygiella*, Adelanthaceae), on account of the presence of a few teeth on the bracts. Recent research has made it clear that it is not related to this primarily tropical family, but instead belongs in Scapaniaceae (A. A. Vilnet et al. 2010).

SELECTED REFERENCES. A. A. Vilnet, N. A. Konstantinova, and A. V. Troitsky. 2010. Molecular insight on phylogeny and systematics of the Lophoziaaceae, Scapaniaceae, Gymnomitriaceae and Jungermanniaceae. Arctoa 19: 31--50.

1. *Biantheridium undulifolium* (Nees) Konstantinova & Vilnet, *Arctoa* 18: 67. 2009 [2010]

Jamesoniella schraderi var. *undulifolia* Nees, *Naturg. Eur. Leberm.* 1: 306. 1833; *Jamesoniella undulifolia* (Nees) Müller Frib., *Crossogyna undulifolia* (Nees) Schljakov

Plants with shoots 1--3 cm x 1--1.5 mm. **Stems** 225--275 μm diam.; branches long; cortical cells 14--20 μm with thin walls, medullary cells slightly larger. **Leaves** imbricate, orbicular, wider than long, 0.8--0.85 x 0.95--1.1 mm, slightly concave, the larger leaves tending to be undulate; margins broadly rounded, entire, emarginate leaves occasional; median leaf cells 22--26 x 25--34 μm ; marginal cells 20--25 μm ; cuticle faintly verruculose; cell walls slightly thickened; trigones present, occasionally slightly bulging; oil bodies 6--12 per cell, spherical to ellipsoid, 4--5 x 6--8 μm , granular. **Underleaves** when present lanceolate or of slime papillae. **Androecia** terminal becoming intercalary; bracts in 4--6 pairs, imbricate, concave with an incurved tooth at dorsal base; antheridia two per bract, stalk 4-seriate. **Gynoecia** (frequently fertile) terminal on main shoot with large somewhat undulate subtending leaves; bracts large, up to 800 x 1200 μm , undulate, similar to distal leaves with small, obscure teeth on margins; bracteole free, large (to 650 μm), lanceolate with 1--2 teeth at base; perianth ovoid-oblong, inflated, contracted to plicate mouth with small 1--2 celled teeth or crenulate margin formed by elongate fingerlike cells.

Peaty soil in bogs or among mosses on tundra; low to high elevations; w and nw Greenland; Que.; n Europe; Asia (Russian Far East, Siberia).

The name *Jamesoniella schraderi* (Mart.) Schiffner has often been misapplied to this species.

5. LOPHOZIA (Dumortier) Dumortier, *Recueil Observ. Jungerm.*, 17. 1835 [Greek *lophos*, crest, spike, alluding to angular ends of lobes]

Vadim Bakalin

Jungermannia sect. *Lophozia* Dumortier, *Syll. Jungerm.*, 52. 1831; *Isopaches* H. Buch, *Lophoziosis* Konstant. & Vilnet, *Obtusifolium* S. W. Arnell, *Oleolophozia* L. Söderström, *Protolophozia* (R. M. Schuster) Schljakov

Plants ca. 3--50 x 0.4--3 mm, prostrate to ascending, from pale green to rusty brown and purplish. **Stems** 0.1--0.5 mm in diameter, sparsely branching, transverse section with microcellous layer to $1/2 \times$ stem thickness or not differentiated; rhizoids sparse to common, in indistinct fascicles, colorless to pale brown. **Leaves** succubous, inserted at various angles, distant to imbricate, spreading to appressed, flat to concave, divided by variously shaped sinus into 2(--3--4) lobes; lobes entire; cells commonly collenchymatous, walls usually thin, but sometimes thickened; oil bodies 2--40 per cell, biconcentric or not; underleaves commonly absent. **Specialized asexual reproduction** by gemmae in masses at apices of leaf-lobes or shoots, absent in some species. **Sexual condition** mainly dioicous, rarely autoicous or paroicous. **Androecia** intercalary, 1--4-androus, antheridial stalk 1--2-seriate. **Gynoecia** terminal, female bracts in 1 pair. **Perianth** exerted $1/2--3/4 \times$ its length, mainly cylindric, complicated at mouth, mouth dentate to ciliate and lobulate; perigynium totally absent. **Capsule** oval, walls 3--5-stratose,

exterior wall with nodular thickenings, interior wall with annular thickenings, reddish brown. **Elaters** 2-spiraled, reddish brown. **Spores** spheric, 7--18 μm , papillose, dark brownish.

Species ca. 60 (23 in the flora): North America, Central America, South America, Eurasia, Africa, Australia, Oceania, Antarctica.

SELECTED REFERENCES Bakalin V.A. 2005. Monograficheskaya obrabotka roda *Lophozia* (Dumort.) Dumort. s. str. Moscow. Hong W. S. 2002. The distribution of *Lophozia* in North America west of the hundredth meridian. *Lindbergia*. 27: 49--62. Schuster R. M. 1969. *Lophozia* (Dumort.) Dumort. In: R. M. Schuster. 1969. Hepaticae and Anthocerotae of North America. New York and London. Vol. 2.

1. Stem cross section with microcellous layer near ventral side.

2. Leaf lobes obtuse to rounded, cells of midleaf with many (to 50) small oil-bodies, underleaves filiform, commonly present but early deciduous, rarely absent, capsule wall (4--5)-stratose . . . 5e. *Lophozia* subg. *Obtusifolium*, p. XX (in part)

2. Leaf lobes acute, or leaves only slightly retuse, cells of midleaf with (1--3)--40 oil bodies per cell, underleaves mainly absent, if present then simple, lanceolate, nearly the same width as stem, not deciduous, capsule wall 3(--4)-stratose.

3. Cells of midleaf usually 25--35 μm wide; gemmae colorless to red and purplish, rarely brown (if brown, then plants whitish, gemmae with long persistent, single, commonly biconcentric oil-body), perianth complicated at mouth, dentate to ciliate along margin . . . 5a. *Lophozia* subg. *Lophozia*, p. XX

3. Cells of midleaf usually 18--22 μm wide; gemmae brown; perianth narrowed to the mouth, mouth dentate, commonly ornamented by sharply elongated cells . . . 5c. *Lophozia* subg. *Sudeticae*, p. XX

1. Stem cross section lacking a microcellous layer near ventral side.

4. Leaves subtransversely inserted, imbricate, stem only 0.10--0.15 mm in diameter, underleaves always absent . . . 5b. *Lophozia* subg. *Isopaches*, p. XX

4. Leaves inserted at various angles, not imbricate, stem as a rule more than 0.2 mm in diameter, underleaves present or absent.

5. Leaves 2--3(--4)-lobed, obliquely inserted, underleaves more or less regular in shape, plants monoicous, gemmae absent . . . 5d. *Lophozia* subg. *Protolophozia*, p. XX

5. Leaves 2--3-lobed, obliquely to subhorizontally inserted, underleaves commonly irregular, plants dioicous, gemmae present, sometimes absent, but in that case leaves nearly horizontally inserted and 2-lobate.

6. Leaves almost horizontally inserted, 2-lobed, lobes obtuse to rounded . . . 5e. *Lophozia* subg. *Obtusifolium*, p. XX (in part)

6. Leaves obliquely to subtransversely inserted, 2--3(--4)-lobed, acute . . . 5c. *Lophozia* subg. *Sudeticae*, p. XX

5a. *Lophozia* (Dumortier) Dumortier subg. *Lophozia*

Plants ca. 4--40 x 0.6--3 mm, ascending to prostrate, pale green-whitish to yellowish green, brown and purplish brown. **Stems** 0.1--0.5 mm in diameter, sparsely branching, transverse

section with microcellous layer to $1/2 \times$ stem thickness, frequently present, but sometimes nearly absent depending on growth habit or ecological condition, outer cells of stem in cross section not or slightly thickened. **Leaves** transversely to subhorizontally inserted, more or less distant, spreading, 2(3--4)-lobed; cuticle smooth to papillose; underleaves rarely present, simple, lanceolate, nearly the same length as leaves. **Specialized asexual reproduction** by angular gemmae, with slightly to sharply thickened angles, colorless to red, occurring in all species. **Sexual condition** dioicous, rarely monoicous or paroicous. **Capsule** oval, wall 3(--4)-stratose, **Spores** spheric, 9--18 μm .

Species 22 (17 in the flora): North America, South America, Eurasia, Africa, Australia, Oceania, Antarctica.

1. Stems in cross section with thickened superficial cell walls along margin; mature gemmae colorless to greenish; antheridial bracts with entire margins . . . 5a.1. *Lophozia* sect. *Lophozia*, p. XX

1. Stems in cross section with thin cell walls throughout; mature gemmae red, reddish, carrot-red, brown, brown-orange to purplish; antheridial bracts sometimes with additional antical teeth . . . 5a.2. *Lophozia* sect. *Excisae*, p. XX

5a.1. *Lophozia* sect. *Lophozia*

Lophozia sect. *Guttulatae* Schljakov; *Lophozia* sect. *Heteromorpha* R. M. Schuster; *Lophozia* sect. *Savicziae* Bakalin

Plants ca. 4--40 x 0.6--2 mm, ascending to prostrate, pale green-whitish to yellowish-green, brown and purplish-brown. **Stems** with outer cells in cross section slightly thickened. **Leaves** transversely to subhorizontally inserted, more or less distant, spreading, 2(--4)-lobed, oil-bodies biconcentric or not; cuticle smooth to papillose. **Specialized asexual reproduction** by colorless to greenish gemmae [brownish]. **Sexual condition** dioicous [monoicous]. **Antheridial** bracts with entire margins.

Species ca. 14 (10 in the flora): North America, Eurasia, Antarctica.

1. Leaves commonly 2--3-lobed, crispate-undulate; gemmae colorless, but sometimes violet. . . 3. *Lophozia heteromorpha*

1. Leaves uniformly 2-lobed, only very rarely 3-lobed, flattened to concave but margin neither undulate nor crispate; gemmae colorless to greenish, rarely with rose or brownish tinge.

2. Leaves only shallowly retuse at apex, base distinctly decurrent dorsally; perianth fusiform . . . 4. *Lophozia pacifica*

2. Leaves clearly lobed with acute to weakly acute lobes, base not decurrent dorsally, perianth cylindrical to subclavate.

3. Plants whitish, ascending; leaves erect-spreading with lobes deflexed from shoot apex; ventral side of stem brownish or the same color as the dorsal; epixylous . . . 1.
Lophozia ascendens

3. Plants greenish to brown and purplish, prostrate to erect in dense patches; leaf lobes erect or rarely deflexed; ventral side of stem brown to purplish; epixylous or not.

4. Plants generally bright-green, more rarely yellowish, particularly when epixylous; mature leaves longer than wide.

5. Leaves flattened, leaf insertion line nearly straight, leaf lobes near apex deflexed. . . 7. *Lophozia silvicola*

5. Leaves grooved, leaf insertion line incurved from very oblique on ventral side to subtransverse dorsally, leaf lobes near apex upturned.

6. Midleaf cells ca. 22--26 μm wide with bulging trigones, near margin sometimes confluent; cuticle commonly striolate . . . 2.
Lophozia guttulata

6. Midleaf cells ca. 22--33 μm wide, trigones triangular to convex, or if cell width less than 26 μm then trigones concave; cuticle commonly smooth.

7. Midleaf cells commonly more than 26 μm wide, trigones triangular to convex, oil-bodies biconcentric; perianth with teeth more than (3--4) cells in length . . . 8. *Lophozia silvicoloides*

7. Midleaf cells commonly less than 26 μm wide, trigones concave, oil-bodies non-biconcentric; perianth with 1--2(--5)-celled teeth . . . 9. *Lophozia ventricosa*

4. Plants generally yellow-brownish to brown, purplish and rusty-red; mature leaves wider than long.

8. Leaves grooved, leaf base semi-sheathing and leaf insertion line incurved from very oblique ventrally to subtransverse dorsally; leaf lobes near apex turned up to form ob-pyriform cap. . . . 9. *Lophozia ventricosa*

8. Leaves flattened or cape-shaped but not grooved and base not semi-sheathing base, leaf insertion line nearly straight, leaf lobes near apex slightly incurved inside, leaves not forming ob-pyriform cap.

9. Leaves without trace of red or purple pigmentation, even dorsally.

10. Leaves obliquely inserted, frequently with deeply brownish colored leaf lobes near apex; oil-bodies biconcentric 6.

Lophozia schusterana

10. Leaves subtransversely inserted, pigmentation of leaf lobes not different; oil-bodies non-biconcentric.... 10. *Lophozia wenzelii*

9. Leaves commonly with red, purple or purplish pigmentation, at least dorsally.

11. Midleaf cells mostly wider than 29 μm ; gemmae penta- to polygonal with protruding angles; oil-bodies commonly more than 20 per cell, at least 50% of them biconcentric 5. *Lophozia savicziae*

11. Midleaf cells mostly narrower than 29 μm ; gemmae 3--4(--5)-angular with protruding angles; oil-bodies commonly less than 20 per cell, biconcentric.... 7. *Lophozia silvicola*

Key to living perianthous plants

1. Oil-bodies biconcentric.

2. Perianth mouth lacinate or ciliate, with cilia to (3--4)--6 cells in length.... 8. *Lophozia silvicoloides*

2. Perianth mouth dentate to shortly lacinate, with cilia not more than 3(--4) cells in length.

3. Oil-bodies more than 20 per cell, smooth, some homogenous non-biconcentric (not more than 50%); leaves subtransversely inserted....5. *Lophozia savicziae*

3. Oil-bodies less than 20 per cell, granulate; leaves obliquely to subhorizontally inserted.

4. Leaves mostly flattened and longer than wide; Arctic to Boreal zones....
7. *Lophozia silvicola*

4. Leaves concave, wider than long; chiefly Arctic ... 6. *Lophozia schusterana*

1. Oil-bodies non-biconcentric.

5. Perianth fusiform; leaves retuse, not distinctly 2-lobed.... 4. *Lophozia pacifica*

5. Perianth cylindric to subclavate; leaves always distinctly lobed.

6. Perianth mouth laciniate to ciliate-laciniate with cilia more than (4--5) cells in length.... 1. *Lophozia ascendens*

6. Perianth mouth dentate to ciliate with cilia shorter than 4 cells in length.

7. Leaves polymorphous 2--3(--4)-lobed, lanceolate, underleaves occasionally present; gemmae and distal portion of perianth sometimes with violet tint.... 3. *Lophozia heteromorpha*

7. Leaves uniformly 2(--3)-lobed; underleaves absent; no violet tint in gemmae or distal portion of perianth.

8. Leaves subtransversely inserted and oriented, strongly concave to cupped, wider than long; shoots not red pigmented.... 10. *Lophozia wenzelii*

8. Leaves obliquely inserted and oriented (rarely subtransversely, but then longer than wide), flattened to grooved, rarely concave, wider than long to longer than wide; shoots often reddish pigmented.

9. Leaves longer than wide, characteristically grooved, trigones strongly convex to bulging; leaf cuticle sometimes striolate; perianth mouth ciliate with cilia 3--4 cells length 2. *Lophozia guttulata*

9. Leaves wider than long (occasionally longer than wide, but then trigones concave and leaves flattened), flattened to concave and grooved, trigones concave to convex; leaf cuticle smooth; perianth mouth dentate or ciliate with cilia 3(--5) cells in length.... 9. *Lophozia ventricosa*

1. *Lophozia ascendens* (Warnstorf) R. M. Schuster, *Bryologist*, 55: 180. 1952

Sphenolobus ascendens Warnstorf, *Hedwigia* 57: 63. 1915; *Lophozia ciliata* Damsholt, Soederstroem & Weibull

Plants ca. 4--10 x 0.6--1 mm, ascending, very rarely prostrate, pale green-whitish and yellowish white. **Stems** 0.15--0.35 mm in diameter, sparsely branching, transverse section with microcellous layer to $1/4 \times$ stem thickness, sometimes absent in attenuate tips; rhizoids sparse to common, in indistinct fascicles, colorless to pale brownish. **Leaves** transversely inserted, distant, spreading, erect-spreading at the ends of lobes, deflexed away from the stem, flat, rectangular to ovate, 0.5--0.7 x 0.3--0.6 mm, 2-lobed, equal lobes divided by U-shaped to crescentic sinus descending to $1/4$ -- $2/5 \times$ leaf length; lobes entire, angular to horn-like; cells of midleaf rectangular to polygonal, 23--28 x 20--25 μm , in base to 40 μm ; cuticle smooth, walls thin, trigones small, triangulate to slightly convex; oil bodies 4--10(--14) per cell, spheric to ovoid, 3--5 x 4--8 μm , finely granular, grayish, non-biconcentric; underleaves rarely present, lanceolate, nearly the same length with leaves. **Specialized asexual reproduction** by gemmae in masses at apices of leaf-lobes, greenish to colorless, commonly triangular to rectangular in outline, (12--15--22 x 11--17 μm , 2-celled, with slightly thickened angles. **Sexual condition** dioicous. **Androecia** intercalary, often with gemmae at tips, male bracts 2 pairs, similar to leaves but inflated in the base, 1-androus, antheridial stalk 1-seriate. **Gynoecia** terminal, female bracts in 1 pair, rectangular to trapezoidal, sometimes dentate, ca. 0.6 x 0.35--0.7 mm, divided to $1/3 \times$ length, connate; bracteole present, lanceolate, sometimes shortly 2-lobed to $1/3 \times$ length, ca. 0.5 x 0.2--0.3 mm, connate with one of bracts to $2/3 \times$ length. **Perianth** exerted to $3/4 \times$ length, cylindrical to slightly rhomboidal, complicated at mouth, mouth ciliate to lobulate with lobules and cilia to 7--8 cells in length, generally 1-stratose. **Seta** 5 mm, capsule oval, wall 3-stratose, exterior wall with nodular thickenings, interior wall with annular thickenings, reddish brown. **Spores** spheric, 9--11 μm .

Decaying wood, predominantly wet dark coniferous forests (*Picea*, *Abies*, etc.), sometimes bark of decaying trees; 0--3200 m; Alta., B.C., Nfld. and Labr. (Nfld.), N.W.T., N.S., Ont., Que., Yukon; Alaska, Colo., Idaho, Maine, Mich., Minn., Mont., N.H., N.Y., Oreg., S.Dak., Vt., Wash., Wis., Wyo.; n Eurasia.

2. *Lophozia guttulata* (Lindberg & Arnell) Evans, Proc. Washington Acad. Sci. 2: 302. 1900

Jungermannia guttulata Lindberg & Arnell, Musci As.-Bor. 51. 1889; *Lophozia longiflora* (Nees) Schiffn. var. *guttulata* (Lindb. & Arnell) Schljakov

Plants ca. 3--10 x 0.8--1 mm, prostrate, yellowish pale green to brownish light green. **Stems** 0.1--0.4 mm in diameter, sparsely branching, transverse section with microcellous layer to $1/5$ -- $1/4 \times$ stem thickness, ventral surface brown-purple to purple-brown-blackish; rhizoids sparse to common, in indistinct fascicles, colorless to purplish near origin area. **Leaves** obliquely inserted, insertion line incurved from nearly horizontal on ventral side to nearly transverse on the dorsal, distant to imbricate, spreading, turn up at the ends of lobes, slightly lengthways sulcate, rectangular, 0.7--1 x 0.5--0.6 mm, 2-lobed, subequal lobes divided by angular to gibbous sinus descending to $1/5$ -- $1/4 \times$ leaf length; lobes entire, triangular to curving; cells of midleaf 4--5-angular, 25--27 x 22--25 μm , in base to 25--30(--35) x 25 μm ; cuticle smooth to papillose, walls thin, trigones bulging, sometimes confluent; oil bodies 4--10(--12) per cell, spheric to ovoid, 4--5 x 5--10 μm , finely granular, grayish, non-biconcentric; underleaves absent. **Specialized asexual reproduction** by gemmae in masses at apices of shoots, sometimes absent, greenish to colorless,

commonly triangular to rectangular, (12--15--22 x 11--17 μm , 2-celled, with slightly thickened angles. **Sexual condition** dioicous. **Androecia** intercalary, male bracts in 2--3 pairs, similar to leaves but inflated basally, 1(--2)-androus, antheridial stalk 1-seriate. **Gynoecia** terminal, female bracts in 1 pair, obovate to rectangular, entire, 1.2--1.3 x 0.8--1 mm, divided to $1/3$ length, connate; bracteole present, lanceolate to narrowly rectangular and shortly 2-lobed to $1/3$ length, connate with one of bracts to $1/3$ length. **Perianth** exerted to $2/3$ length, cylindric to somewhat clavate, complicated at mouth, mouth dentate to ciliate with cilia to 4(--8) cells in length, generally 1-stratose. **Seta** ca. 5 mm, capsule oval, walls 3-stratose, exterior walls with nodular thickenings, interior walls with annular thickenings, reddish brown. **Spores** 11--13 μm in diameter.

Decaying wood, mainly dark coniferous forests, wet peaty soil or peat-moss in boggy areas, more rarely humus soil and fine-grained ground along lakes in forested areas; 0--3300 m; Alta., B.C., Man., Nfld. and Labr., N.W.T., N.S., Ont., Que., Yukon; Alaska, Calif., Colo., Conn., Idaho, Iowa, Maine, Mass., Mich., Minn., Mont., N.H., N.Mex., N.Y., Oreg., Utah, Vt., Wash., Wis., Wyo.; Central America; n Eurasia.

3. Lophozia heteromorpha R. M. Schuster & Damsholt, Schuster, Hep. Anth. North Amer. 2: 507. 1969

Plants ca. 5--25 x 1--2 mm, prostrate, pale to bright green or greenish brown and blackish, frequently with violet-colored tips. **Stems** 0.3--0.8 mm in diameter, sparsely branching, transverse section with microcellous layer to $1/3$ stem thickness or absent, ventral surface brown to black-brown and purple-brown; rhizoids sparse to common, in indistinct fascicles, colorless to pale violet near origin area. **Leaves** obliquely inserted, distant to contiguous, spreading, undulate, polymorphous from orbicular to subquadrate and trapezoidal, 0.8--1 x 0.8--1.4 mm, 2--3(--4)-lobed, subequal lobes divided by crescentic to gibbous sinus descending to $1/5$ -- $2/5$ leaf length; lobes entire, triangular to curving; cells of midleaf 4--5-angular, 18--30(--35) x 17--27 μm ; cuticle smooth, walls thin to somewhat thickened, trigones distinct, triangular to concave, oil bodies unknown; underleaves sometimes present, filiform to lanceolate to 200--300 μm . **Specialized asexual reproduction** rare, by gemmae at apices of shoots, colorless to pale violet, commonly triangular to rectangular in outline, 14--19 x 14--24 μm , (1--2)-celled, with slightly thickened angles. **Sexual condition** dioicous. **Androecia** unknown. **Gynoecia** terminal, female bracts in 1 pair, obovate to rectangular, entire, 1.2--1.3 x 0.8--1 mm, divided to $1/3$ length into 2--3 lobes, connate, bracteole present, lanceolate to narrowly rectangular and shortly 2-lobed to $1/3$ length, connate with one of bracts to $2/3$ length. **Perianth** exerted to $2/3$ length, cylindric to somewhat ob-clavate, complicated at mouth, mouth dentate with few teeth 2(--3) cells in length, generally 1-stratose. Other features unknown.

Among mosses and liverworts in dense patches, as well as in disturbed areas, data on ecology very incomplete; elevation unknown; Greenland; Alaska; n Eurasia

4. Lophozia pacifica Bakalin, Bryologist 114: 302, fig. 1. 2011

Plants 10--20 x 2--2.3 mm, prostrate to ascending, bright green to yellowish green without traces of reddish coloration except ventral side of stem, dorsiventrally flattened. **Stems** 0.35--0.4 mm in

diameter, sparsely branching, transverse section with microcellous layer to $\frac{1}{5}$ stem thickness or absent, ventral surface red-brown; rhizoids sparse to nearly absent, originated in dorsal side of stem at right angle. **Leaves** obliquely to nearly horizontally inserted, clearly decurrent on dorsal side, obliquely spreading, somewhat concave with lobes incurved inwardly, distant, oval to widely ovate, 1.2--1.5 x 1.3--1.4 mm, shallowly retuse; cells of midleaf 4--5-angular, 28--35 x 25--28 μm , basally to 50 μm ; cuticle smooth but at base distinctly verrucose, walls thin, trigones convex to bulging; oil-bodies 4--8 per cell, finely papillose, irregularly ellipsoidal, 4--5.5 x 3--4.7 μm ; underleaves absent. **Specialized asexual reproduction** by solitary gemmae at apices of shoot, greenish to colorless, commonly 4--5-angular in outline, 15--25 x 15--20 μm , 2-celled, with slightly thickened angles. **Sexual condition** dioicous. **Androecia** intercalary, male bracts 2--3 pairs, trapezoidal, inflated in the base, 1--2-anded, 90--120 μm , antheridial stalk 1-seriate. **Gynoecia** terminal with one or two innovations, female bracts in 1 pair, obovate, entire, 1.3--1.5 x 1.1-1.3 mm, divided $\frac{1}{8}$ length into 2 lobes by crescentic sinus, connate, bracteole present, lanceolate ca. 1.3 x 0.35-0.45 mm, connate with one of bracts to $\frac{2}{3}$ length. **Perianth** exerted to $\frac{5}{6}$ length, fusiform, constricted to mouth, ca. 3 x 1 mm, mouth dentate with sharply elongated 1-celled teeth, generally 1-stratose. **Sporophyte** unknown.

Ecology incompletely known, apparently confined to tundra belt of low mountains, wet mineral to humus soil, partial shade to full sun; 1500--1800 m; Wash.

5. *Lophozia savicziae* Schljakov, Novosti Sist. Nizsh. Rast. 10: 299. 1973

Lophozia silvicola var. *grandiretis* H. Buch & S.W. Arnell; *L. ventricosa* var. *grandiretis* (H. Buch & S.W. Arnell) R. M. Schuster & Damsholt

Plants ca. 5--20 x 1.5--2 mm, usually prostrate, rarely ascending, yellow-brown to rusty brown. **Stems** (0.2--0.25--0.3 mm in diameter, sometimes slightly transversely oval in cross section, sparsely branching, transverse section with microcellous layer to $\frac{2}{3}$ stem thickness, red-brown in color, ventral surface of stem brown-purple to purple-brown, or purple-black; rhizoids sparse to common, in indistinct fascicles, colorless to purplish near origin area. **Leaves** subtransversely inserted, insertion line more or less straight, distant to imbricate, spreading, turned up at the ends of lobes, strongly concave to cup-shaped, orbicular to trapezoidal, 0.8--1.1 x 1.1--1.5 mm, sometimes 2-stratose in base to $\frac{1}{10}$ length, 2-lobed, unequal lobes divided by crescentic to angular or gibbous sinus descending to $\frac{1}{5}$ leaf length; lobes entire, triangular to curving; cells variable in size, in midleaf 5--6-angular, 25--45 x 25--40 μm , but mostly exceeding 30 μm wide; cuticle smooth to papillose, walls thin, trigones usually bulging, sometimes confluent; oil bodies 15--40 per cell, spheric to ovoid, ca. 2--5 μm , finely granular to nearly smooth, light bluish, more than 60% of oil-bodies are biconcentric; underleaves very rarely present, lanceolate. **Specialized asexual reproduction** by gemmae in masses at apices of shoots, sometimes absent, greenish to colorless, commonly 5-angular, more rarely 4-angular to polygonal in outline, (18--22--30 x 15--30(--33) μm , 1--2-celled, with strongly thickened and protruding angles. **Sexual condition** dioicous. **Androecia** unknown. **Gynoecia** terminal, female bracts in 1 pair, obovate to rectangular, entire, 1.2--1.5 x 1.5--2 mm, divided to $\frac{1}{3}$ length into 2--3 lobes, rarely connate; bracteole narrowly rectangular, shortly 2-lobed to $\frac{1}{4}$ length, 0.8--0.9 x 1.1--1.2 mm, connate with one of bracts to $\frac{1}{3}$ length. **Perianth** exerted to $\frac{5}{6}$ length,

cylindric to somewhat subclavate, complicated at mouth, mouth dentate to shortly lobulate with teeth to 2(--3) cells in length, generally 1-stratose. **Sporophyte** unknown.

Northern tundra, sometimes in northern mountains, among mosses or in pure mats in wet habitats, mainly places with percolated water, often somewhat alkaline rocks; 0--1000 m; Greenland; Alaska; n Eurasia.

6. *Lophozia schusterana* Schljakov, Novosti Sist. Nizsh. Rast. 12: 320. 1975

Plants ca. 5--30 x 1--2 mm, prostrate to erect, in dense patches, yellowish to pale green and peculiarly brownish at the tips, commonly laterally compressed. **Stems** 0.3--0.48 mm in diameter, sparsely branching, transverse section with microcellous layer to $1/3$ stem thickness, ventral surface brownish purple to reddish brown; rhizoids sparse to rarely common, in indistinct fascicles, colorless to purplish near origin area. **Leaves** obliquely to horizontally inserted, distant to imbricate, commonly appressed, rarely spreading, rectangular to nearly orbicular, antically secund, 0.9--1.1 x 0.9--1.2 mm, 2-lobed, subequal lobes divided by crescentic to angular sinus descending to $1/5$ -- $1/4$ leaf length; lobes entire, triangular to curving; cells of midleaf 4--5-angular, 24--32 x 23--26 μ m; cuticle smooth, walls thin, trigones convex to bulging; oil bodies 8--18(--30) per cell, spheric to ovoid, 4--6 x 5--10 μ m, finely granular, grayish, biconcentric; underleaves absent. **Specialized asexual reproduction** by gemmae in masses at apices of shoots, sometimes absent, greenish to colorless, commonly triangular to rectangular in outline, (18--21--25 x 18--20 μ m, 1--2-celled, with slightly thickened angles. **Sexual condition** dioicous. **Androecia** intercalary, male bracts 2--3 pairs, similar to leaves but inflated in the base, 1(--2)-androus, antheridial stalk 1--2-seriate. **Gynoecia** terminal, female bracts in 1 pair, obovate to rectangular, entire, 1.2--1.3 x 0.8--1 mm, divided to $1/3$ length into 2--4 lobes, connate; bracteole present, lanceolate, connate with one of bracts to $1/3$ length, 1--1.5 x 0.5 mm. **Perianth** exerted to $2/3$ length, cylindric to somewhat clavate, complicated at mouth, mouth dentate with remote 1--2-celled teeth, generally 1-stratose. **Sporophyte** unknown.

Restricted to tundra zone, not exceeding mountain tundra belt in boreal (taiga) areas, overhanging rock in snow-bed communities, crevices, among mosses and other liverworts, rarely submerged in temporary streams or on moist soil on steep slopes; 0--2200 m; Greenland; B.C., Nfld. and Labr. (Labr.), Nunavut; Alaska, Mich.; n Eurasia.

Lophozia schusterana is *L. groenlandica* in the sense of Schuster (1969) but not *Jungermannia groenlandica* Nees.

7. *Lophozia silvicola* H. Buch, Rep. 18. Scand. Naturalist Congr., 228. 1929

Lophozia ventricosa var. *silvicola* (H. Buch) Jones

Plants ca. 10--20 x 1.7--2(--2.2) mm, prostrate to creeping, yellowish green to bright green. **Stems** 0.25--0.3 mm in diameter, sparsely branching, transverse section with microcellous layer to $1/3$ -- $2/3$ stem thickness, ventral surface brown to purple-brown; rhizoids sparse to common, in indistinct fascicles, colorless to yellowish and brownish. **Leaves** commonly very obliquely inserted but rarely subtransverse, insertion line nearly straight, distant, spreading, flattened,

deflexed from the apex, rectangular, 1--1.5 x 0.7--1 mm, 2-lobed, subequal lobes divided by crescentic to angular sinus descending to $1/5$ -- $1/4$ x leaf length; lobes entire, acute, triangular to almost horn-like, sometimes ending by 2 superposed cells; cells of midleaf 5--6-angular, 28--30 x 25--30 μm , in base to 50 μm ; cuticle smooth, walls thin, trigones concave, triangular to rarely bulging; oil bodies 7--18(--20) per cell, spheric to ovoid, 4--7 x 5--10 μm , finely granular, grayish, biconcentric; underleaves absent. **Specialized asexual reproduction** by gemmae in masses at lobe apices of distal leaf, greenish to colorless, commonly 3--5-angular in outline, 15--18 x 12--17 μm , 2-celled, with thickened angles. **Sexual condition** dioicous. **Androecia** intercalary, male bracts 2--4 pairs, similar to leaves but inflated in the base, 1--2-androus, antheridial stalk 2-seriate. **Gynoecia** terminal, innovations common, female bracts in 1 pair, obovate to rectangular, entire, 1.5--2(--2.2) x 1.3--1.7 mm, divided to $1/3$ x length into 2--3 lobes, connate, bracteole present, lanceolate, connate with one of bracts to $1/3$ x length. **Perianth** exerted to $2/3$ x length, cylindric, complicated at mouth, mouth dentate with 2--3-celled teeth, generally 1-stratose. **Seta** ca. 10--15 mm, capsule oval, wall 3--4-stratose, exterior wall with nodular thickenings, interior wall with annular thickenings, reddish brown. **Elaters** ca. 60 x 5--6 μm . **Spores** spheric, 10--13 μm , papillose, dark brown.

Dark coniferous forest communities on decaying wood and in moss mats on forest floor, wet places, also tundra and boggy areas over moss mats, humus and rarely pure peat, steep slopes with disturbed vegetation cover; 0--2900 m; Greenland; Alta., B.C., Nfld. and Labr., N.W.T., N.S., Ont., Que.; Alaska, Calif., Colo., Idaho, Maine, Mass., Mich., Minn., N.H., N.Y., N.C., Tenn., Vt., Va., Wash., Wis., Wyo.; n Eurasia.

Note: A specimen determined as *Lophozia silvicola* from California, Fresno, J. R. Shevock & D. A. York 13948 (MO) was recently redetermined by D. Wagner as *Lophozia murmanica* Kaal.

8. *Lophozia silvicoloides* N. Kitagawa, J. Hattori Bot. Lab. 28: 276. 1965

Plants ca. 5--30 x 0.5--2(--2.5) mm, prostrate with ascending tips, pale to bright green sometimes brownish. **Stems** 0.25--0.4 mm in diameter, sparsely branching, transverse section with microcellous layer to $1/3$ -- $2/3$ x stem thickness, ventral surface red-brown to purple-black; rhizoids sparse to common, in indistinct fascicles, colorless to reddish near origin area. **Leaves** commonly obliquely inserted, rarely subtransverse, insertion line curved from nearly horizontal on dorsal surface to subtransverse on the ventral, distant, spreading, flattened, deflexed from the apex, rectangular to ovoid, 0.5--1.3 x 0.4--1.2 mm, 2-lobed, subequal (dorsally secund) lobes divided by crescentic to angular and U-shaped sinus descending to $1/4$ -- $1/3$ (-- $2/5$) x leaf length; lobes entire, acute to somewhat acute, triangular to curving; cells of midleaf 5--6-angular, (22--28--40 x 25--45 μm , in base to 50 μm ; cuticle smooth, walls thin to slightly thickened, trigones triangular to bulging; oil bodies 10--20(--25) per cell, spheric to ovoid, 3--7 x 3--8 μm , finely granular, light bluish, biconcentric; underleaves absent. **Specialized asexual reproduction** by gemmae in masses at lobe apices of distal leaf, greenish to colorless, commonly 3--5-angular in outline, 15--28 x 13--27 μm , 2-celled, with slightly thickened angles. **Sexual condition** dioicous. **Androecia** intercalary, male bracts 3--5 pairs, similar to leaves but inflated in the base, 1--2-androus, antheridial stalk 2-seriate. **Gynoecia** terminal, innovations common, female bracts in 1 pair, obovate to rectangular, entire, 1.5--2(--2.2) x 1.3--1.7 mm, divided to $1/3$ x length into 2--4 lobes, connate, bracteole present, lanceolate, connate with one

of bracts to $\frac{1}{3}$ length. **Perianth** exerted to $\frac{4}{5}$ length, cylindrical, to subclavate, 3--4 x 1--1.2 mm, complicated at mouth, mouth dentate to ciliate and lobulate with lobules 2--3 cell in base and 5--7 cells in length, generally 1-stratose. **Spores** 13--18 μm in diameter, papillose, dark brown.

Arctic-montane species with suboceanic distribution, tundra, over mosses in dense patches in mesic areas; 0--100 m; Alaska; n Eurasia.

9. *Lophozia ventricosa* (Dickson) Dumortier, Recueil Observ. Jungerm., 17. 1835

Jungermannia ventricosa Dickson, Pl. Crypt. Brit., fasc. 2: 14. 1790; *Lophozia ehrhartiana* (F. Weber) Inoue & Steere, *Lophozia subapiculata* R. M. Schuster & Damsholt

Plants ca. 10--20 x 1--2(--2.2) mm, prostrate to ascending and nearly erect in dense patches, bright green to yellowish green, yellowish brown, and reddish brown. **Stems** 0.13--0.3 mm in diameter, sometimes slightly transversely oval, sparsely branching, transverse section with microcellous layer to $\frac{1}{3}$ -- $\frac{1}{4}$ stem thickness, ventral surface brown to purple-brown; rhizoids sparse to common, in indistinct fascicles, colorless to yellowish and brownish near origin. **Leaves** commonly obliquely inserted but rarely subtransverse, insertion line curved from nearly horizontal on dorsal surface to subtransverse on the ventral, distant, spreading, concave to flattened, turned up the apex, rectangular, obtrapezoidal to suborbicular, 0.8--1.2 x 0.75--1.2 mm, usually 2-lobed, unequal or subequal lobes divided by angular to gibbous sinus descending to $\frac{1}{5}$ -- $\frac{1}{4}$ leaf length; lobes entire, acute, triangular to curving, sometimes ending by 2 superposed cells; cells of midleaf 5--7-angular, 25--31 x 23--28 μm , in base to 45 μm ; cuticle smooth, rarely verrucose, walls thin, trigones concave, triangular to bulging; oil bodies 7--18(--20) per cell, spheric to ovoid, 4--7 x 5--10 μm , finely granular, grayish, non-biconcentric; underleaves absent. **Specialized asexual reproduction** by gemmae in masses at apex of shoots, greenish to colorless, commonly 3--4(--5)-angular in outline, 15--25 x 12--20 μm , (1--2)-celled, with slightly thickened angles. **Sexual condition** dioicous. **Androecia** intercalary, male bracts 2--3 pairs, similar to leaves but inflated in the base, 1--2-androus, antheridial stalk 1--2-seriate. **Gynoecia** terminal, female bracts in 1 pair, obovate to rectangular and obtrapezoidal, entire, 1--2 x 1--2 mm, divided to $\frac{1}{3}$ length into 2--3 lobes, connate; bracteole present, lanceolate, connate with one of bracts to $\frac{1}{3}$ length. **Perianth** exerted to $\frac{3}{4}$ length, cylindrical, complicated at mouth, mouth dentate with 2--4(--5)-celled teeth, generally 1-stratose. **Seta** ca. 10--15 mm, capsule oval, wall 3--4-stratose, exterior wall with nodular thickenings, interior wall with annular thickenings, reddish brown. **Elaters** ca. 100--175 x 6--8 μm . **Spores** spheric, 10--13 μm , papillose, dark brown to reddish brown.

Varieties 2 (2 in the flora): North America, Eurasia, Antarctica.

Lophozia . ventricosa var. *confusa* R. M. Schuster and *L ventricosa* var. *rigida* R. M. Schuster are minor variants not recognized here.

1. Leaves longer than wide, divided by angular to U-shaped sinus, trigones in midleaf cells concave . . . 9a. *Lophozia ventricosa* var. *ventricosa*

1. Leaves wider than long, divided by gibbous sinus, trigones in midleaf cells convex to bulging .
 . . 9b. *Lophozia ventricosa* var. *longiflora*

9a. *Lophozia ventricosa* var. *ventricosa*

Plants ca. 10--20 x 1.8--2 mm, prostrate to ascending and nearly erect in dense patches, bright green to yellowish green, yellowish brown. **Stems** with ventral surface brown to purple-brown. **Leaves** spreading, flattened or rarely undulate, turned up the apex, rectangular, obtrapezoidal to orbicular, 0.8--1.2 x 0.75--1.2 mm, usually 2-lobed, unequal or subequal lobes divided by angular sinus descending to $1/5$ -- $1/4$ x leaf length; lobes entire, acute, triangular, sometimes ending by 2 superposed cells; cuticle smooth, walls thin, trigones concave to triangular.

Among mosses, lichens, dwarf-shrubs, steep slopes in mesic conditions, tundra zone or belt, decaying wood, forest floor, places with disturbed vegetation cover (both native and anthropogenic), also crevices of various rock, banks of streams and lakes; 0--3300; Greenland; Alta., B.C., N.B., Nfld. and Labr., N.W.T., N.S., Nunavut, Ont., Que., Yukon; Alaska, Ariz., Calif., Colo., Conn., Idaho, Maine, Mass., Mich., Minn., Mont., Nev., N.H., N.Y., N.C., Oreg., R.I., Tenn., Utah, Wash., Wis., Wyo.; n Eurasia.

9b. *Lophozia ventricosa* var. *longiflora* (Nees) Macoun, Cat. Canad. Pl. 7: 17. 1902

Jungermannia longiflora Nees, Naturg. Eur. Leberm., 2: 95. 1836; *Lophozia longiflora* (Nees) Schiffn.

Plants ca. 10--20 x 1.8--2.2 mm, prostrate to ascending and nearly erect in dense patches, yellowish green to yellowish brown and reddish brown. **Stems** ventral surface brown to purple-brown. **Leaves** spreading, concave to cup-shaped, turned to the apex, orbicular, 0.8--1.2 x 0.75--1.2 mm, usually 2-lobed, subequal lobes by angular or more usually gibbous sinus descending to $1/5$ -- $1/4$ x leaf length; lobes entire, acute, triangular to curving, walls thin, trigones convex to bulging.

Common in both zonal and mountain tundra, drying pools, among mosses (mainly *Sphagnum*), rarely on rocks, also dark coniferous forest on decaying wood, peaty turfs; 0--4000 m; Greenland; B.C., Nfld. and Labr. (Labr.), Ont., Que.; Alaska, Calif., Colo., Idaho, Maine, Minn., Mont., N.H., Wis.; n Eurasia; Central America; Antarctic.

10. *Lophozia wenzelii* (Nees) Stephani, Spec. Hepat. 2: 127, fig. 135. 1901

Jungermannia wenzelii Nees, Naturgesch. Eur. Leberm., 2: 6, fig. 58. 1836

Plants ca. 5--40 x 0.2--3 mm, erect in dense patches, small form creeping, yellow-brown, rarely with purplish colored tips of shoots (high Arctic phases). **Stems** 0.15--0.5 mm in diameter, sparsely branching, transverse section with microcellous layer to $1/3$ x stem thickness, ventral surface brownish to black-brown, without reddish pigmentation; rhizoids sparse to rarely common, in indistinct fascicles, colorless to brownish near origin area. **Leaves** subtransversely inserted, distant to (more frequent) imbricate, commonly appressed, nearly orbicular, sometimes

antically secund, (0.2--0.3--1(--1.2) x (0.2--0.35--1.3(--1.5) mm, 2-lobed, subequal lobes divided by crescentic to rarely angular sinus descending to $1/5$ -- $1/4$ leaf length; lobes entire, triangular to curving; cells of midleaf 4--6-angular, 20--30(--35) x (15--20--28(30) μm ; cuticle smooth, walls thin, trigones concave to convex; oil bodies (2--4--10(--15) per cell, spheric to ovoid, 4--8 x 5--10 μm , finely granular to almost smooth, grayish, non-biconcentric; underleaves absent. **Specialized asexual reproduction** by gemmae in masses at apices of shoots, sometimes absent, greenish to colorless, in sunny forms some of them can acquire pale rose or slightly brownish pigmentation, commonly triangular to rectangular in outline, (16--20--26(--28) x (12--14--21(--25) μm , 1--2-celled, with slightly thickened angles. **Sexual condition** dioicous. **Androecia** intercalary, male bracts to 15 pairs, but commonly only with 5--6 ones, similar to leaves but inflated in the base, 1--2-androus. **Gynoecia** terminal, female bracts in 1 pair, obovate to transversely rectangular and orbicular, entire, 1.2--1.3 x 1.2--1.5 mm, divided to $1/3$ length into 2--3(--4) lobes, connate; bracteole present, lanceolate to 2-lobate, connate with one of bracts to $2/3$ length, ca. 1 x 0.5 mm. **Perianth** exerted to $2/3$ length, cylindric, complicated at mouth, mouth dentate with remote 1--2-celled teeth, generally 1-stratose. **Spores** 10--13 μm in diameter.

Varieties 5 (3 in the flora): North America, Eurasia.

1. Leaves subtransversely to obliquely inserted, divided by angular to gibbous sinus into unequal lobes . . . 10b. *Lophozia wenzelii* var. *groenlandica*

1. Leaves subtransversely inserted, divided by angular or crescentic sinus into equal to subequal lobes.

2. Plants erect in dense patches, wider than 1 mm, rich peat moss bogs . . . 10a. *Lophozia wenzelii* var. *wenzelii*

2. Plants creeping to ascending, narrower than 0.8 mm, wet soil . . . 10c. *Lophozia wenzelii* var. *lapponica*

10a. *Lophozia wenzelii* var. *wenzelii*

Plants ca. 5--30 x 1--3 mm, erect in dense patches, yellow-brown. **Stems** 0.3--0.5 mm in diameter, sparsely branching, transverse section with microcellous layer to $1/3$ stem thickness. **Leaves** subtransversely inserted, imbricate, commonly appressed, nearly orbicular, equal lobes divided by crescentic sinus descending to $1/5$ -- $1/4$ leaf length; lobes entire, obtuse.

Sphagnum bogs, wet mossy tundra, among mosses and other liverworts, 0--3500 m; Greenland; Alta., B.C., Nfld. and Labr., N.W.T., Ont., Que., Sask., Yukon; Alaska, Calif., Colo., Idaho, Maine, Mont., N.H., N.Mex., Oreg., Wash., Wyo.; n Eurasia.

All old and many new records of var. *wenzelii* could not be checked, but it is apparent that not less than half of them are misidentifications, mainly of *L. ventricosa*, so the distribution needs additional work.

10b. Lophozia wenzelii var. **groenlandica** (Nees) Bakalin, *Arctoa* 10: 213. 2001

Jungermannia groenlandica Nees in Gottsche, Lindenberg & Nees, *Syn. Hep.*, 114. 1844;
Lophozia groenlandica (Nees in Gottsche, Lindenberg & Nees) Macoun

Plants ca. 5--40 x 1--3 mm, erect in dense patches or creeping on soil, yellow-brown to brown.
Stems 0.3--0.5 mm in diameter, sparsely branching, transverse section with microcellous layer to $\frac{2}{5}$ stem thickness. **Leaves** subtransversely to oblique inserted, imbricate to distant, orbicular or trapezoidal, dorsally secund unequal lobes divided by angular to gibbous sinus descending to $\frac{1}{5}$ - $\frac{1}{4}$ leaf length; lobes entire, triangular.

Dry tops of hummocks in bogs, mesic cliffs, places with disturbed vegetation cover, humus, unforested areas; 0--1800 m; Greenland; B.C.; Alaska, Wash.; n Eurasia.

10c. Lophozia wenzelii var. **lapponica** H. Buch & S.W. Arnell, *Svensk Bot. Tidskr.* 44(1): 81. 1950

Plants ca. 5--30 x 0.2--0.8 mm, creeping on soil, yellow-brown to brown and blackish, rarely with purple tips. **Stems** 0.15--0.3 mm in diameter, sparsely branching, transverse section with microcellous layer to $\frac{2}{5}$ stem thickness. **Leaves** subtransversely inserted, imbricate, orbicular, subequal lobes divided by angular sinus descending to $\frac{1}{4}$ leaf length; lobes entire, triangular.

Mainly soil in tundra or tundra belt, rarely dark coniferous forest, damp soil or rocks, 0--2700 m, Greenland; N.W.T., Que.; Calif.; n Eurasia.

5a.2. LOPHOZIA sect. **EXCISAE** R. M. Schuster, *Hep. Anth. North Amer.*, 2: 511. 1969

Plants ca. 4--50 x 0.6--2 mm, ascending to prostrate, pale green-whitish to yellowish green, brown and purplish brown. **Stems** with outer cells in cross section thin. **Leaves** transversely to subhorizontally inserted, more or less distant, spreading, 2-lobed in exceptional cases 3--4-lobed (some leaves on the stem); oil-bodies non-biconcentric; cuticle smooth. **Specialized asexual reproduction** by gemmae: mature always red to purple, immature sometimes greenish to colorless. **Sexual condition** dioicous, paroicous, autoicous; antheridial bracts frequently with additional tooth near dorsal side.

Species 8 (7 in the flora): North America, South America, Eurasia, Africa, Australia, Oceania, Antarctica.

1. Plants monoicous or rarely dioicous and if so lax-leaved, soft-textured and bearing (2--3--4-celled gemmae . . . 11. *Lophozia excisa*

1. Plants dioicous, not soft-textured, gemmae (1--2-celled.

2. Plants whitish, small, restricted calcareous sites; oil bodies in leaf cells sometimes biconcentric; gemmae brown with commonly long persistent 1--2 oil bodies per cell . . . 15. *Lophozia perssonii*

2. Plants green to brownish and brown, not whitish, growing in calcareous sites or not; oil bodies in leaf cells never biconcentric; gemmae red to green, rarely brownish, with many quickly disappear oil-bodies.

3. Plants attenuate with spreading to erect-spreading leaves; ends of lobes deflexed from the apex . . . 12. *Lophozia longidens*

3. Plants prostrate to erect in dense patches, never ascending; lobes flattened, sometimes crispate-undulate.

4. Gemmae greenish to brownish, concolorous with lobe ends pigmentation; calcareous sites . . . 14. *Lophozia pellucida*

4. Gemmae greenish (immature only) to deep red and purplish, in color different from that of lobe ends; acidic sites, rarely calcareous.

5. Plants dark brown; gemmae 5--6-polygonal purple; cells of midleaf mostly more than 30 μm wide . . . 17. *Lophozia rubrigemma*

5. Plants deep-green to brownish, rarely dark brown; gemmae 3--5-angular, rarely 6-angular, but in this case not purple; cells of midleaf mostly less than 30 μm wide.

6. Lobes divided by crescentic or U-shaped sinus, gemmae rusty-red . . . 16. *Lophozia polaris*

6. Lobes divided by angular to gibbous sinus, mature gemmae purple.

7. Oil-bodies granulate . . . 13. *Lophozia propagulifera*

7. Oil-bodies botryoidal . . . 16b. *Lophozia polaris* var. *sphagnorum*

11. *Lophozia excisa* (Dickson) Dumortier, Recueil Observ. Jungerm., 17. 1835

Jungermannia excisa Dickson, Pl. Crypt. Brit., fasc. 3: 11. 1793; *Lophoziosis excisa* (Dicks.) Konstant. & Vilnet

Plants ca. 10--30 x 1--2.1 mm, prostrate, rarely ascending, yellowish green to yellow-brownish or rarely bright green. **Stems** 0.15--0.4 mm in diameter, sparsely branching, transverse section with microcellous layer to $1/4$ -- $2/3$ x stem thickness, sometimes undifferentiated, ventral surface brown to purple-brown; rhizoids dense, in indistinct fascicles, colorless to brownish near origin area. **Leaves** obliquely inserted, but sometimes line insertion becomes almost transverse on dorsal side, distant to imbricate, spreading to erect-spreading or laterally appressed to the stem,

turn up at the ends of lobes, sometimes slightly undulate, rectangular to trapezoidal, 0.55--1 x 0.55--1 mm, 2-lobed, subequal to unequal acute lobes divided by angular to gibbous sinus descending to $1/4$ -- $1/3$ leaf length; lobes entire, triangular to curving; cells of midleaf 4--5-angular, 25--32 x 23--30 μm , in base to ca. 40 x 35 μm ; cuticle smooth, walls thin, trigones concave and small, rarely bulging; oil bodies 10--30 per cell, spheric to oval, 3--5 μm in diameter to 3--5 x 4--8 μm if ellipsoidal, granulate, colorless, non-biconcentric; underleaves absent. **Specialized asexual reproduction** by gemmae sparse at apices of shoots, frequently absent, greenish when immature to red and purple, commonly 4--5-angular in outline with distinctly protruding angles, 25--38 x 20--28 μm , 2(--3--4)-celled. **Sexual condition** parocious. **Androecia** below gynoecia, male bracts 2--3 pairs, similar to leaves but inflated in the base, sometimes with additional tooth near dorsal base, 1--3(--4)-androus. **Gynoecia** terminal sometimes with subfloral innovations, female bracts in 1 pair, obovate to rectangular, entire to messy dentate or undulate, 1.2--1.3 x 0.8--1.3 mm, divided to $1/3$ leaf length into 3--4 lobes, connate, bracteole present, lanceolate to narrowly rectangular and shortly 2-lobed to $1/3$ leaf length, connate with one of bracts to $2/3$ leaf length. **Perianth** exerted to $2/3$ leaf length, cylindric to somewhat pyriform, complicated at mouth, mouth dentate with sparse 1--2-celled teeth, generally 1-stratose. **Seta** ca. 5 mm, capsule oval, wall 3-stratose, exterior wall with nodular thickenings, interior wall with annular thickenings, reddish brown. **Spores** 12--20 μm in diameter.

Varieties 3 (2 in the flora): North America, Eurasia, South America, Australia, Antarctica (?).

1. Plants somewhat rigid; stem cross section orbicular or nearly orbicular; specialized asexual reproduction by 2-celled gemmae . . . 11a. *Lophozia excisa* var. *excisa*

1. Plants soft-textured; stem cross-section transversely oval; specialized asexual reproduction by 3--4-celled gemmae . . . 11b. *Lophozia excisa* var. *elegans*

11a. *Lophozia excisa* var. *excisa*

Lophozia excisa var. *infusata* R. M. Schuster; *L. excisa* var. *succulenta* R. M. Schuster; *Lophozia excisa* var. *infusata* (R. M. Schuster & Damsholt) Konstant. & Vilnet, *Lophozia excisa* var. *succulenta* (R. M. Schuster & Damsholt) Konstant. & Vilnet

Plants somewhat rigid. **Stems** cross-section orbicular or nearly orbicular. **Specialized asexual reproduction** by 2-celled gemmae.

Tundra, also frequent in mesic conditions in forested areas, exposed and wet soil, among mosses in dense mats, dry humus, snow-bed and snow-fed habitats, steep slopes to river; 0--3300 m; Greenland; Alta., B.C., Man., Nfld. and Labr., N.W.T., N.S., Nunavut, Ont., Que., Yukon; Alaska, Calif., Colo., Conn., Idaho, Maine, Mich., Minn., Mont., N.H., N.J., N.Y., N.C., Oreg., R.I., Wash., Wis., Wyo.; South America; Eurasia; Australia; Oceania (New Zealand); Antarctica.

11b. *Lophozia excisa* var. *elegans* R. M. Schuster, Hep. Anth. North Amer., 2: 522. 1969

Lophozia excisa var. *elegans* (R. M. Schuster) Konstantinova & Vilnet

Plants soft-textured. **Stems** cross-section transversely oval. **Specialized asexual reproduction** by 3--4-celled gemmae.

Northern tundra, mesic conditions among mosses; 0--100 m; Greenland; Nunavut; n Eurasia.

12. Lophozia longidens (Lindberg) Macoun, Geol. Survey Canada: Cat. Canad. Pl. 7: 18. 1902

Jungermannia longidens Lindberg, Bot. Not., 27. 1877; *Lophoziosis longidens* (Lindberg) Konstantinova & Vilnet

Plants ca. 5--15 x 0.6--1 mm, ascending, rarely prostrate, green to bright green, rarely brownish. **Stems** 0.17--0.35 mm in diameter, sparsely branching, transverse section with microcellous layer to $1/3--1/2$ stem thickness, sometimes absent in attenuate tips; rhizoids sparse to common, in indistinct fascicles, colorless to pale brownish near origin. **Leaves** transversely or (rarely, in shady forms) oblique inserted, distant, spreading, erect-spreading at the ends of lobes, deflected away from the stem, flattened, rectangular to ovate, 0.4--0.8 x 0.3--0.55 mm, 2(--3)-lobed, equal lobes divided by U-shaped to semilunate sinus descending to $1/3--1/4$ leaf length; lobes entire, angulate to horn-like; cells of midleaf rectangular to rarely pentagonal, 23--27 x 22--26 μm , in base to 30 μm ; cuticle smooth, walls thin, trigones small, concave to triangular; oil bodies 3--12(--17) per cell, spheric, 3--7 μm in diameter to ovoid, 3--5 x 4--9 μm , finely granular, nearly colorless to grayish, non-biconcentric; underleaves absent. **Specialized asexual reproduction** by gemmae in masses at apices of leaf-lobes, red-brown to brownish and chestnut, rarely greenish in shade forms, commonly 3--4(--5)-angular in outline, 20--30(--40) x 13--24(--36) μm , (1--2)-celled, with slightly thickened angles. **Sexual condition** dioicous. **Androecia** intercalary, often with gemmae at tips, male bracts 3 pairs, similar to leaves but inflated in the base, 1-androus, antheridial stalk 1-seriate. **Gynoecia** terminal with subfloral innovations, female bracts in 1 pair, rectangular to trapezoidal, sometimes dentate, but commonly entire, ca. 0.6 x 0.35--0.7 mm, divided to $1/3$ length into 2--4 lobes, connate; bracteole present, lanceolate, sometimes shortly 2-lobed to $1/3$ length, ca. 0.5 x 0.2--0.3 mm, connate with one of bracts to $2/3$ length. **Perianth** exerted to $3/4$ length, ca. 2--2.5 x 0.7 mm, cylindric, complicated at mouth, mouth ciliate to lobulate with lobules and cilia to 5--7 cells in length, generally 1-stratose. **Seta** 5 mm, capsule oval, walls 3-stratose, exterior walls with nodular thickenings, interior walls with annular thickenings, reddish brown. **Elaters** ca. 100--120 x 7.5 μm . **Spores** spheric, 11--13 μm .

Tundra to dark coniferous forest, rarely broad-leaved woods, on rocks of various composition, soil, among mosses, decaying wood, steep slopes to waterways, also places with disturbed vegetation cover; 0--3500 m; Greenland; Alta., B.C., Nfld. and Labr., N.W.T., N.S., Ont., Que., Yukon; Alaska, Colo., Conn., Idaho, Maine, Mass., Mich., Minn., Mont., N.H., N.Y., Oreg., Vt., Wash., Wis., Wyo.; n Eurasia.

A minor tason, *Lophozia longidens* var. *arctica* (R. M. Schuster) Vaňá & L. Söderstr. Is known for Greenland, distinguished from the typical variety by larger leaf cells with more oil bodies and larger gemmae.

13. Lophozia propagulifera (Gottsche) Stephani, Exped. Antarct. Belge, Bot. 3: 4. 1901.

Jungermannia propagulifera Gottsche, Neumayer, Int. Polarforsch., Deutsch. Exped. 2: 451. 1890; *Lophozia latifolia* R. M. Schuster; *Lophoziosis propagulifera* (Gottsche) Konstantinova & Vilnet

Plants ca. 10--30 x 1.2--1.7 mm, prostrate, but frequently ascending, yellowish brown to yellowish green or rarely bright green. **Stems** 0.25--0.35 mm in diameter, sparsely branching, slightly transversely oval in cross section, with microcellous layer to $1/2 \times$ stem thickness, cell walls distinctly thickened along margin, ventral surface brown to purple-brown; rhizoids sparse to dense, in indistinct fascicles, grayish. **Leaves** obliquely to nearly horizontal inserted, appressed to the stem, ends of lobes turned to apex, sometimes slightly undulate, rectangular to trapezoidal, 0.5--0.7 x 0.5--0.8 mm, 2-lobed, subequal to unequal, acute, lobes divided by angular to gibbous sinus descending to $1/3--2/5 \times$ leaf length; lobes entire, triangular to curving; cells of midleaf 5--6-angular, 28--32 x 23--30(--32) μm , in base to ca. 43 μm in diameter; cuticle smooth, walls thin to somewhat thick, trigones concave and small; oil bodies 4--25 per cell, spheric 3--6 μm in diameter to oval 3--5 x 4--8 μm , granulate, colorless, non-biconcentric; underleaves absent. **Specialized asexual reproduction** by gemmae sparse at apices of shoots, frequently absent, greenish (commonly as admixture, but sometimes to 90%) to purple, commonly 4--5-angular in outline with weakly protruding angles, 25--38 x 20--28 μm , 2-celled. **Sexual condition** dioicous, autoicous and (rarely) paroicous. **Androecia** intercalary, male bracts 4(--5) pairs, similar to leaves but inflated in the base, sometimes with additional tooth near dorsal base, 1--2-androus. **Gynoecia** terminal sometimes with subfloral innovations, female bracts in 1 pair, obovate to rectangular, entire to undulate, 1.2--1.3 x 0.8--1.3 mm, divided to $1/3 \times$ length into 3--4 lobes, connate; bracteole present, lanceolate to narrowly rectangular and shortly 2-lobed to $1/3 \times$ length, connate with one of bracts to $2/3 \times$ length. **Perianth** exerted to $3/4 \times$ length, cylindrical to rhomboidal, complicated at mouth, mouth dentate with sparse 1--2-celled teeth, generally 1-stratose. **Seta** ca. 5 mm, capsule oval, wall 3-stratose, exterior wall with nodular thickenings, interior wall with annular thickenings, reddish brown. **Spores** 12--20 μm in diameter.

Damp moss mats, tundra or more rarely forested areas, bogs and rocky cliffs, exposed or partly shaded places; elevation unknown; Greenland; Nfld. and Labr. (Labr.), N.W.T., Nunavut; Alaska, Calif., Minn., Wash.; Eurasia; Antarctica.

14. *Lophozia pellucida* R. M. Schuster, Canad. J. Bot. 39: 978. 1961

Lophozia pellucida var. *minor* R. M. Schuster, *Lophoziosis pellucida* (R. M. Schuster) Konstantinova & Vilnet

Plants ca. 5--30 x 1--2.5 mm, prostrate, yellowish brown to yellowish green or rarely brown. **Stems** 0.2--0.45 mm in diameter, sparsely branching, slightly transversely oval in cross section, with microcellous layer to $1/4 \times$ stem thickness, commonly weakly developed and indistinct, cell walls distinctly thickened along margin, ventral surface brown; rhizoids sparse to dense, in indistinct fascicles, colorless. **Leaves** obliquely to nearly horizontal inserted, distant and spreading, rarely appressed to the stem, flattened, ends of lobes peculiarly more deeply colored

(commonly distinctly brownish), trapezoidal to transversely oval, 0.5--1.3 x 0.5--1.5 mm, 2-lobed, subequal to unequal acute lobes divided by angular to gibbous sinus descending to $1/3$ -- $2/5$ leaf length; lobes entire, triangular to curving; cells of midleaf 4--6-polygonal, 30--45 x 25--40 μm , in base to ca. 50 μm in diameter; cuticle smooth, walls thin to somewhat thickened, trigones concave and small; oil bodies (5--9)--18(--25) per cell, spheric 4--5.5 μm in diameter to oval 6.5--9 x 4.5--5.5 μm , finely granulate, colorless, non-biconcentric; underleaves absent.

Specialized asexual reproduction by gemmae sparse at apices of shoots and lobe ends, frequently absent, concolorous with leaf lobes, green to brownish or brown, (22--25)--40(--45) x (20--22)--32(--36) μm , 2-celled. **Sexual condition** dioicous [autoicous and paroicous].

Androecia intercalary, male bracts 3--4 pairs, similar to leaves but inflated in the base, rarely with additional tooth near dorsal base. **Gynoecia** terminal sometimes with subfloral innovations, female bracts in 1 pair, obovate to rectangular, entire to undulate, 1.2--1.3 x 0.8--1.8 mm, divided to $1/3$ leaf length into 2--4 lobes, connate, bracteole present, lanceolate to narrowly rectangular and shortly 2-lobed to $1/3$ leaf length, connate with one of bracts to $2/3$ leaf length.

Perianth exerted to $3/4$ leaf length, cylindrical to rhomboidal, complicated at mouth, mouth dentate with sparse 1--2-celled teeth, generally 1-stratose. **Sporophyte** unknown.

Soil, disturbed vegetation cover, also on mosses in crumbly mats, mainly confined to calcareous sites, rarely on acid silty deposits; elevation unknown; Greenland; Alta., Nunavut; Alaska; n Eurasia.

15. Lophozia perssonii H. Buch & S.W. Arnell in: H Buch, Bot. Not., 381. 1944

Oleolophozia perssonii (H. Buch & S. W. Arnell) L. Söderstr., DeRoo & Hedd.

Plants ca. 2--10 x 0.5--1 mm, ascending, pale green, brownish to whitish. **Stems** 0.15--0.3 mm in diameter, sparsely branching, orbicular in cross section, with microcellous layer to $2/5$ stem thickness, cell walls very thin, ventral surface brownish or undifferentiated; rhizoids sparse to dense, in indistinct fascicles, grayish. **Leaves** subtransversely to slightly oblique inserted, imbricate or spreading, ends of lobes turned to apex or deflexed away the stem, rectangular to ovate, 0.4--0.7 x 0.3--0.7 mm, 2-lobed, subequal lobes divided by U-shaped or crescentic sinus descending to $1/6$ -- $1/3$ leaf length; lobes entire, triangular to somewhat curved-triangular; cells of midleaf 5--6-angular, 21--40 x 20--30 μm ; cuticle smooth, walls very thin, trigones concave, very small or absent; oil bodies 3--10 per cell, spheric 3--8 μm in diameter to oval 3--5 x 4--9 μm , granulate, colorless, sometimes biconcentric; underleaves absent. **Specialized asexual reproduction** by gemmae common at shoot apices, brown to brownish, commonly 3--5-angular in outline with weakly protruding angles, 15--21(--23) x 12--15(--19) μm , 1--2-celled, with long-persistent large single oil-body in each cell. **Sexual condition** dioicous. **Androecia** intercalary, male bracts 2--3 pairs, similar to leaves but concave at the base, 1--2-androus. **Gynoecia** terminal, female bracts in 1 pair, obovate to rectangular, entire to weakly dentate, divided to $1/3$ leaf length into 2 lobes, connate, bracteole present, lanceolate to narrowly rectangular and shortly 2-lobed to $1/3$ leaf length, connate with one of bracts to $2/3$ leaf length. **Perianth** exerted to $2/3$ leaf length, cylindrical to cone-shaped, complicated at mouth, mouth ciliate-dentate with sparse 5--7-celled cilia, generally 1-stratose. **Capsule** oval, exterior walls with nodular thickenings, interior walls with annular thickenings, reddish brown. **Spores** 14--18 μm in diameter.

Mesic to xeric limestone cliffs or dry basic clayish deposits; 0--200 m; Greenland; Alaska; n Europe.

16. Lophozia polaris (R. M. Schuster) R. M. Schuster & Damsholt, Meddel. Gronland 199: 131. 1974

Lophozia alpestris ssp. *polaris* R. M. Schuster, Hep. Anth. North Amer., 2: 614. 1969;
Lophozioopsis polaris (R. M. Schust.) Konstant. & Vilnet

Plants ca. 3--30 x 0.6--2.5 mm, prostrate, but frequently ascending in dense patches, green to yellowish brown-green and brown. **Stems** 0.25--0.5 mm in diameter, sparsely branching, slightly transversely oval in cross section, with microcellous layer to $1/2 \times$ stem thickness, cell walls distinctly thickened along margin, ventral surface brown to purple-brown; rhizoids sparse to nearly absent, in indistinct fascicles, grayish. **Leaves** obliquely to nearly horizontally inserted, appressed to the stem, ends of lobes upturned, sometimes slightly undulate, rectangular to trapezoidal, 0.4--1.3 x 0.4--1.6 mm, 2-lobed, subequal nearly acute to obtuse lobes divided by crescentic, U-shaped or angular sinus descending to $1/6--1/4(--1/3--2/5) \times$ leaf length; lobes entire, triangular; cells of midleaf 5--6-angular, (20--25--35 x (18--23--35 μm); cuticle smooth, walls thin to somewhat thick, trigones concave and small; oil bodies (3--6--20 per cell; underleaves absent. **Specialized asexual reproduction** by gemmae sparse at apices of shoots, rarely on ends of lobes before apex, frequently absent, red, rusty-red to carrot-red, commonly 4--5-angular in outline with weakly protruding angles, 18--32 x 14--28 μm , 1--2-celled. **Sexual condition** dioicous. **Androecia** intercalary, male bracts 4--7 pairs, similar to leaves but inflated in the base. **Gynoecia** terminal without subfloral innovations, female bracts in 1 pair, trapezoidal to transversely oval, entire to slightly undulate, ca. 1.5 x 2 mm, divided to $1/3--2/5 \times$ length into 3--4 lobes with strongly deflexed sinus, connate, bracteole present, 2-lobed to $1/3 \times$ length, connate with one or both bracts to $1/2 \times$ the length. **Perianth** exerted to $1/2 \times$ its length, cylindrical to cone-shaped, complicated at mouth, mouth dentate with sparse 1--2-celled teeth, generally 1-stratose. **Sporophytes** unknown.

Varieties 2 (2 in the flora): North America, n Eurasia.

1. Lobes divided by crescentic or U-shaped sinus descending to $1/6--1/4 \times$ leaf length; oil-bodies 6--17 per cell, granulate, spheric 3.5--6(--8) μm in diameter to oval (4--6--8 x 3--6 μm
16a. *Lophozia polaris* var. *polaris*

1. Lobes divided by angular to somewhat gibbous sinus descending to $1/3--2/5 \times$ leaf length; oil-bodies 3--14 per cell, botryoidal, oval 3--5 x 4--6 μm 16b. *Lophozia polaris* var. *sphagnorum*

16a. Lophozia polaris var. **polaris**

Leaves 2-lobed, subequal nearly acute to obtuse lobes divided by crescentic or U-shaped sinus descending to $1/6--1/4 \times$ leaf length; oil-bodies 6--17 per cell, granulate, spheric 3.5--6(--8) μm in diameter to oval (4--6--8 x 3--6 μm .

Predominantly basic conditions over mosses and other liverworts in wet places, frequently in percolate water, more rarely cliffs and ledges, banks of sluggishly flowing streams; 0--1000 m; Greenland; Nunavut; Alaska; n Eurasia.

16b. *Lophozia polaris* var. *sphagnorum* (R. M. Schuster) R. M. Schuster & Damsholt, Meddel. Gronland 199: 134. 1974

Lophozia alpestris ssp. *polaris* f. *sphagnorum* R. M. Schuster, Hep. Anth. North Amer. 2: 619. 1969; *Lophoziaopsis polaris* var. *sphagnorum* (R. M. Schust.) Konstant. & Vilnet

Leaves 2-lobed, subequal nearly acute to obtuse lobes divided by angular to somewhat gibbous sinus descending to $1/3--2/5$ leaf length; oil-bodies 3--14 per cell, botryoidal, oval 3--5 x 4--6 μm .

Mostly over *Sphagnum*, bogs and mossy tundras; 0--500 m; Greenland; Alaska; n Eurasia.

17. *Lophozia rubrigemma* R. M. Schuster, Hep. Anth. North Amer. 2: 621. 1969

Lophoziaopsis rubrigemma (R. M. Schust.) Konstant. & Vilnet

Plants ca. 3--10 x 0.7--1 mm, prostrate, but frequently ascending in dense patches, yellowish brown to brown. **Stems** 0.25--0.3 mm in diameter, sparsely branching, slightly transversely oval in cross section, microcellous layer to $1/2$ stem thickness, cell walls distinctly thickened along margin, ventral surface brown to purple-brown; rhizoids sparse to nearly absent, in indistinct fascicles, grayish. **Leaves** obliquely inserted, distant, spreading to appressed to the stem and slightly concave, ends of lobes turned away of stem, sometimes slightly undulate, rectangular to trapezoidal, 0.4--1.2 x 0.4--1.2 mm, 2-lobed, subequal nearly acute to obtuse lobes divided by crescentic, U-shaped or angular sinus descending to $1/3--2/5$ leaf length; lobes entire, triangular; cells of midleaf polygonal to orbicular, (28--30--38(--43) x 28--36(--45) μm ; cuticle smooth, walls somewhat thick, trigones concave and small; oil bodies 10--30 per cell, granulate, spheric 3--5 μm in diameter to shortly oval 3--4.5 x 4--9 μm ; underleaves absent. **Specialized asexual reproduction** by gemmae sparse at apices of shoots, rarely on ends of lobes before apex, red to deep purple-red, commonly (5--6)-polygonal in outline with protruding angles, 25--35 x 25--30 μm , 2-celled. **Sexual condition** dioicous. **Androecia** unknown. **Gynoecia** terminal without subfloral innovations, female bracts in 1 pair, trapezoidal to transversely oval, entire to slightly undulate, ca. 1.5 x 2 mm, divided to $1/4--1/3$ length into 2--3(--4) lobes with strongly deflexed sinus, connate, bracteole present, 2-lobed with sinus descending to $1/3$ length, connate with both of bracts to $1/2$ length. **Perianth** exerted to $1/2$ its length, cylindrical to conic, complicated at mouth, mouth dentate with sparse 2--3-celled teeth, generally 1-stratose. **Sporophytes** unknown.

Acidophilic, common in Arctic deserts, more rare but also common in some areas of tundra, exposed sites, places with disturbed or light vegetation cover; elevation unknown; Greenland; Nunavut; Alaska; n Eurasia.

XXb. LOPHOZIA subg. ISOPACHES (H. Buch) R. M. Schuster, Amer. Midl. Nat. 45(1): 56. 1951

Isopaches H. Buch, Mem Soc. F. Fl. Fenn., 8: 283. 1933

Plants ca. 3--15 x 0.6--3 mm, prostrate, loosely adhering to substratum, decolorated to deep green, but commonly brown to reddish brown. **Stems** 0.1--0.15 mm in diameter, sparsely branching, transverse section without microcellous layer, outer cells of stem in cross section clearly thickened, rhizoids conspicuously large. **Leaves** transversely to obliquely inserted, imbricate, rarely distant, spreading, 2-lobed; cuticle smooth; underleaves rarely present, simple, lanceolate, nearly the same length with leaves. **Specialized asexual reproduction** by angular gemmae, with sharply thickened angles. **Sexual condition** paroicous, autoicous to dioicous. **Capsule** oval, walls 2(--3)-stratose, **Spores** 12--15 μm in diameter.

Species 4 (3 in the flora): North America, South America, Eurasia, Australia, Oceania (New Zealand).

1. Plants monoicous (occasionally paroicous, very rarely with antheridial subfloral innovations), female bracts entire, perianth mouth lobulate-ciliate, plants strongly aromatic . . . 19. *Lophozia bicrenata*

1. Plants dioicous, female bracts dentate or entire, perianth mouth crenulate or ciliate-dentate, plants not or slightly aromatic.

2. Female bracts entire, perianth mouth crenulate . . . 20. *Lophozia decolorans*

2. Female bracts sharply dentate, perianth mouth ciliate-dentate . . . 18. *Lophozia alboviridis*

18. Lophozia alboviridis R. M. Schuster, Hep. Anth. North Amer. 2: 487. 1969
Isopaches alboviridis (R. M. Schust.) Schljakov

Plants ca. 3--7 x 0.7--1 mm, prostrate, whitish green to brownish and purplish in upper area. **Stems** 0.11--0.15 mm in diameter, sparsely branching, orbicular in cross section, with homogenous inner cells, outer cells distinctly thickened, ventral surface brownish; rhizoids dense, in tangled fascicles, colorless to brownish, closely attaching plants to substratum. **Leaves** subtransversely to obliquely inserted, appressed to the stem, imbricate, ends of lobes turned to apex, orbicular, 0.5--0.7 x 0.5--0.7 mm, 2-lobed, subequal to unequal acute lobes divided by angular to crescentic sinus descending to $1/4$ leaf length; lobes entire, triangular, acute; cells of midleaf 5--6-angular with rounded angles, 20--24 x 20--28 μm ; cuticle smooth, walls clearly thick, trigones concave and small; oil bodies 10--15 per cell, spheric ca. 5--6 μm in diameter to oval 5--6 x 6--8(--10) μm , granulate, colorless, non-biconcentric; underleaves absent. **Specialized asexual reproduction** by gemmae common at apices of shoots, reddish yellow to reddish brown, commonly 4--5-angular in outline, with protruding angles, 24--38 x 24--28 μm ,

2-celled, red-brown. **Sexual condition** dioicous. **Androecia** unknown. **Gynoecia** terminal, female bracts in 1 pair, obovate to nearly orbicular, sharply dentate, divided to $\frac{1}{3}$ length into 2--3(--4) lobes, connate, bracteole present, lanceolate, connate with one of bracts to $\frac{2}{3}$ length. **Perianth** mouth lobulate and spinose-dentate with teeth to 2(--3) cells in length, generally 1-stratose. **Sporophyte** unknown.

Bare, cleaved soil in Arctic polygonal tundra (data incomplete); Greenland; n Eurasia.

19. Lophozia bicrenata (Schmidel ex Hoffmann) Dumortier, Recueil Observ. Jungerm., 17. 1835

Jungermannia bicrenata Schmidel ex Hoffman, Deutschl. Fl. 2 (addenda), 11. 1796; *Isopaches bicrenatus* (Schmidel ex Hoffm.) H. Buch

Plants ca. 5--10 x 0.4--0.5(--1) mm, prostrate with apex frequently ascending, yellowish green to yellowish brown and deep green. **Stems** 0.11--0.15 mm in diameter, sparsely branching, orbicular in cross section, with homogenous inner cells, outer cells distinctly thickened, ventral surface brownish; rhizoids dense, in tangled fascicles, colorless to brownish, closely attached plants to substratum. **Leaves** subtransversely to obliquely inserted, appressed to the stem, imbricate, ends of lobes turned to apex, orbicular to subquadrate, 0.5--0.7 x 0.7--1 mm, 2-lobed, subequal to unequal acute lobes divided by angular to crescentic sinus descending to $\frac{1}{4}$ leaf length; lobes entire, triangular, acute; cells of midleaf 5--6-angular with rounded angles, 25--35 x 22--27 μm , at base more large, to ca. 40 x 35 μm ; cuticle smooth, walls clearly thick, trigones concave and small; oil bodies (3--6)--12(--15) per cell, spheric ca. 5--8 μm in diameter to oval 5--8 x 6--10(--12) μm , granulate, colorless, non-biconcentric; underleaves absent. **Specialized asexual reproduction** by gemmae common at apices of shoots, reddish yellow to reddish brown, commonly 4--5-angular in outline, with protruding angles, 24--38 x 24--28 μm , 2-celled. **Sexual condition** paroicous, very rarely with androecial subfloral innovations (autoicous). **Androecia** intercalary, male bracts 2--4(--5) pairs, transversely oval inflated in the base, 1--2-androus, stalk 1(--2)-seriate. **Gynoecia** terminal, female bracts in 1 pair, obovate to nearly orbicular, nearly entire, ca. 0.7--1.2 x 0.9 mm, divided to $\frac{1}{3}$ length into 2--3(--4) lobes, connate, bracteole present, lanceolate, sometimes with one additional teeth near base, connate with one of bracts to $\frac{2}{3}$ length. **Perianth** exerted to $\frac{2}{3}$ length, cylindric to cone-shaped, complicated at mouth, mouth lobulate and dentate with teeth to 1--2(--3) cells in length, generally 1-stratose. **Capsule** oval, exterior wall with nodular thickenings, interior wall with annular thickenings, reddish brown. **Elaters** ca. 8 μm in diameter. **Spores** 12--15 μm in diameter.

Fine-grained and sandy soil in various communities except Arctic deserts, mostly mesic conditions, sometimes growing among other liverworts in disturbed areas as well as on rocks covered by thin layer of mineral soil; 0--2700 m; Greenland; B.C., N.B., Nfld. and Labr., N.S., Ont., Que.; Alaska, Colo., Conn., Ga., Idaho, Ill, Ind., Kans., Ky., Maine, Mass., Mich., Minn., Miss., Mo., Nev., N.H., N.J., N.Y., N.C., Ohio, Okla., Oreg., Pa., R.I., S.C., Tenn., Vt., Va., Wash., W.Va., Wis.; Eurasia, Australia; Oceania (New Zealand).

A minor variant, *Lophozia bicrenata* var. *immersa* R. M. Schuster & Damsh., is known from Greenland, differing from the typical variety by thin-walled laminal cells with brownish middle lamellae and retention of oil bodies in all leaves.

20. Lophozia decolorans (Limpricht) Stephani, Spec. Hep. 2: 147. 1902

Jungermannia decolorans Limpricht, Jahresb. Schles. Gesell. Vaterl. Kult. 57: 116. 1880;
Isopaches decolorans (Limpr.) H. Buch

Plants ca. 3--6 x 0.5--0.7 mm, prostrate to semi-immersed into substratum, yellow-brown with decolorate shoot apices. **Stems** 0.11--0.15 mm in diameter, sparsely branching, orbicular in cross section, with homogenous inner cells, outer cells distinctly thickened, ventral surface brownish; rhizoids dense, in tangled fascicles, colorless to brownish, closely attached plants to substratum. **Leaves** subtransversely inserted, appressed to the stem, imbricate, ends of lobes turned to apex, widely ovoid-orbicular, 0.5--0.6 x 0.8--0.8 mm, 2-lobed, subequal to unequal acute lobes divided by U-shaped to crescentic sinus descending to $1/9$ -- $1/8$ leaf length; lobes entire, triangular, acute; cells of midleaf 5--6-angular with rounded angles, 23--30 x 12--23 μm ; cuticle smooth, walls clearly thick at margins, but thinner in middle, trigones absent in margins to convex in midleaf; underleaves absent. **Specialized asexual reproduction** by gemmae common at apices of shoots, reddish, commonly 4--5-angular in outline, with slightly protruding angles, 24--26 x 19--25 μm , 1--2-celled. **Sexual condition** dioicous. **Androecia** intercalary, male bracts 3--5(--7) pairs, transversely oval inflated in the base, 1-androus, stalk 1(--2)-seriate. **Gynoecia** terminal, female bracts in 1 pair, obovate to nearly orbicular, nearly entire, ca. 0.7--0.8 x 1--1.3 mm, divided to $1/4$ length into 2--3 lobes, connate, bracteole present, lanceolate. **Perianth** exerted to $1/2$ length, cylindric to cone-shaped, complicated at mouth, mouth dentate with teeth to 1--2 cells in length, generally 1-stratose. **Spores** 12--15 μm in diameter.

Semi-immersed into soil over granite rocks (only one report for North America); 1600 m; B.C.; Eurasia; Tropical Africa

XXc. Lophozia subg. Sudeticae (Schljakov) Bakalin, Bryologist 114: 310. 2011

Lophozia sect. *Sudeticae* Schljakov, Pechen Mkh Severa SSSR 3: 113. 1980

Plants ca. 5--25 x 0.7--2.2 mm, prostrate, brown to purplish brown, rarely deep brownish green. **Stems** 0.2--0.5 mm in diameter, sparsely branching, transverse section with or without microcellous layer to $1/2$ stem thickness, outer cells of stem in cross section thickened. **Leaves** oblique to subhorizontally inserted, more or less distant to subimbricate, spreading, 2(--3)-lobed; cuticle smooth to papillose; underleaves lanceolate or 2-lobed into 2 narrow lamina, filiform, frequently irregular and nearly absent. **Specialized asexual reproduction** by angular gemmae, with moderately thickened angles, colorless to brown. **Sexual condition** dioicous. **Capsule** oval, wall 3(--4)-stratose, **Spores** spheric, ca. 10 μm .

Species 2 (2 in the flora): North America, Eurasia.

1. Leaves 2--3(--4)-lobed, sinus descending to $1/3$ leaf length, underleaves commonly present . . . 22. *Lophozia debiliformis*

1. Leaves 2-lobed, sinus descending to $1/5$ leaf length, underleaves commonly absent . . . 21. *Lophozia sudetica*

21. *Lophozia sudetica* (Nees ex Huebener) Grolle, Trans. Brit. Bryol. Soc. 6: 262. 1971

Jungermannia sudetica Nees ex Huebener, Hepaticol. Germ., 142. 1834; *Lophozia rufescens* Schljakov, *Barbilophozia rubescens* (R. M. Schust. & Damsholt) Kartt. & L. Söderström, *Barbilophozia sudetica* (Nees ex Huebener) L. Söderström, De Roo & Hedderson.

Plants ca. 5--20 x 1--2(--2.2) mm, prostrate to ascending or erect in dense patches, brownish to rusty brown, rarely with purple tinge or dark green (in shady places). **Stems** 0.2--0.4 mm in diameter, sometimes transversely oval in cross section, ca. 0.3 x 0.4 mm, sparsely branching, transverse section with microcellous layer to $1/3$ stem thickness or absent in southern phases, ventral surface brown to purple-black; rhizoids sparse to nearly absent, in indistinct fascicles, colorless to yellowish and brownish. **Leaves** commonly very obliquely inserted but rarely subtransverse, insertion line nearly straight, distant, spreading to appressed, concave to cup-shaped, turned to apex or to dorsal side, orbicular to trapezoidal-rounded, (0.4--0.6--1.2 x (0.5--0.7--1.3) mm, 2-lobed, subequal lobes divided by crescentic to (rarely) angular sinus descending to $(1/12--1/8--1/5(--1/4))$ leaf length; lobes entire, acute, triangular; cells of midleaf 4--polygonal, 17--25(--27) x 13--22(--28) μm , in base to 40 μm ; cuticle smooth to faintly verruculose, walls thin, trigones concave, triangular to convex; oil bodies (1--2--6(--15) per cell, irregularly oval, 4--7 x 5--9 μm , rarely spheric, 4--7 μm in diameter, very finely papillose, grayish, non-biconcentric; underleaves absent. **Specialized asexual reproduction** by gemmae in masses at apices of distal leaf lobes, rusty-brown, commonly 4--5-angular in outline, 17--22 x 12--15 μm , (1--2)-celled, with slightly thickened angles. **Sexual condition** dioicous. **Androecia** intercalary, male bracts 2(--3) pairs, similar to leaves but inflated in the base, 2(--3)-androus, antheridial stalk 1-seriate at base, but sometimes 2-seriate near spherule. **Gynoecia** terminal, innovations absent, female bracts in 1 pair, oval to ovoid, shallowly 2-lobed, entire, ca. 1.1 x 1 mm, divided to $1/7--1/5$ length into 2 lobes, connate, bracteole present, lanceolate, ca. 0.5--0.2 mm connate with one of bracts to $1/3$ length. **Perianth** exerted to $3/4$ length, cylindrical to clavate and cylindrical-fusiform, complicated at mouth, mouth denticulate to dentate with 2-celled teeth, last cell about 35 μm in length, generally 1-stratose. **Seta** ca. 3--5 mm, capsule oval, walls 3--4-stratose, exterior walls with nodular thickenings, interior walls with annular thickenings, reddish brown. **Elaters** 2-spiral, linear, reddish brown, ca. 100--125 x 7 μm . **Spores** ca. 10 μm in diameter.

Rocks outcrops, shaded soil, among mosses and other liverworts, common in both xeric and mesic conditions, more rarely hygrophilous, but frequent in snow-bed areas, tundra communities, sparse but frequent in some areas in boreal and temperate zones in rock crevices and soil on steep slope; 0--2500 m; Greenland; Alta., B.C., Nfld. and Labr., N.W.T., Nunavut, Ont., Que., Yukon; Alaska, Calif., Colo., Conn., Idaho, Maine, Mass., Mich., Minn., Mont., Nev., N.H., N.Y., Oreg., Utah, Vt., Wash., Wis., Wyo.; Eurasia.

The names *Lophozia alpestris* (Schleicher in Weber) Evans and *Lophozia ehrhartiana* (Weber) Inoue & Steere have both been incorrectly used for this species in the North American literature.

22. *Lophozia debiliformis* R. M. Schuster & Damsholt, *Phytologia* 63(5): 326. 1987

Lophozia debiliformis var. *concolor* R. M. Schuster & Damsholt

Plants ca. 5--25 x 0.7--1(--2) mm, prostrate, nearly soft-textured, green-brownish to brown, apparently without purple tinge. **Stems** 0.25--0.4 mm in diameter, sometimes transversely oval in cross section, ca. 0.3 x 0.4 mm, sparsely branching, transverse section with homogenous cells without microcellous layer, ventral surface brownish; rhizoids sparse to nearly absent, in indistinct fascicles, colorless to yellowish and brownish. **Leaves** commonly obliquely inserted to rarely subtransverse, insertion line nearly straight or incurved from oblique on ventral side to subtransverse on the dorsal, distant, spreading, concave to flattened and undulate, widely ovoid, orbicular to trapezoidal-rounded, (0.4--0.6--1.2 x (0.5--0.7--1.3 mm, 2--3(--4)-lobed, subequal or unequal lobes divided by angular or gibbous to U-shaped sinus descending to $1/5--1/3$ leaf length; lobes entire, acute, triangular; cells of midleaf 4--polygonal, 16--25(--27) x 16--22(--25) μm , in base to 30 μm ; cuticle smooth, walls thin, trigones concave, triangular to convex; oil bodies (2--3--5(--12) per cell, irregularly oval, 6--10 x 4--8 μm , rarely spheric, 4--6 μm in diameter, papillose to rarely smoothed botryoidal, grayish, non-biconcentric; underleaves present, lanceolate or 2-lobed into 2 narrow lamina, frequently irregular and nearly absent. **Specialized asexual reproduction** by gemmae in masses at apices of distal leaf lobes, rusty-brown to brownish white, commonly 4--6-angular in outline, 23--26 x 16--20 μm , (1--2)-celled, with slightly thickened angles. **Sexual condition** dioicous. **Androecia** intercalary, male bracts 2--3(--4) pairs, similar to leaves but inflated in the base, 1(--2)-androus, antheridial stalk 1-seriate. **Gynoeceia** terminal, innovations present, female bracts in 1 pair, oval to ovoid, deeply (2--3)-lobed, entire, but frequently with additional tooth near dorsal base, ca. 0.6 x 0.6 mm, divided to $1/4--2/5$ length into (2--3) lobes, bracteole present, lanceolate, ca. 0.5--0.2 mm connate with one of bracts to $2/3$ length. **Perianth** exerted to $1/2$ length, obovate-clavate, complicated at mouth, mouth denticulate to dentate with 1--2-celled teeth, generally 1-stratose. **Sporophyte** unknown.

Snow-bed habitats, coastal cliffs, thin soil on shaded rocks, tundra zone; 0--1200 m; Greenland; Alaska; Eurasia.

XXd. LOPHOZIA subg. **PROTOLOPHOZIA** R. M. Schuster, *Nova Hedwigia* 15: 472. 1968

Plants ca. 5--25 x 0.7--2.2 mm, prostrate, brown to purplish-brown, rarely deep green-brownish. **Stems** 0.2--0.5 mm in diameter, sparsely branching, transverse section without microcellous layer, outer cells of stem in cross section thin. **Leaves** oblique to subhorizontally inserted, more or less distant to subimbricate, spreading, 2--3-lobed; cuticle smooth to papillose; underleaves lanceolate or 2-lobed into 2 narrow lamina, filiform, sometimes irregular. **Specialized asexual reproduction** not present in our species. **Sexual condition** paroicous. **Capsule** oval, walls 3(--4)-stratose, **Spores** spheric, 10--14 μm .

Species 11 (1 in the flora): North America; Central America; South America; Eurasia; Oceania; Australia, Africa.

23. Lophozia elongata Stephani, Spec. Hep. 2: 128. 1901

Protolophozia elongata (Steph.) Schljakov

Plants ca. 5--20 x 1.1--1.5 mm, prostrate, slightly soft-textured, green to yellowish green and rarely green-brownish, apparently without purple tinge. **Stems** 0.2--0.3 mm in diameter, sometimes transversely oval in cross section, ca. 0.2 x 0.3 mm, sparsely branching, transverse section with homogenous cells without microcellous layer, ventral surface indistinguishable from the dorsal; rhizoids sparse to nearly absent, in indistinct fascicles, nearly colorless. **Leaves** commonly obliquely inserted to rarely subtransverse, insertion line nearly straight or incurved from oblique in ventral side to subtransverse in the dorsal, distant, spreading, concave to flattened and undulate, widely ovoid, orbicular, trapezoidal-rounded or obtapezoidal, (0.4--0.6--0.7 x (0.5--0.6--0.7 mm, 2--3(--4)-lobed, subequal or unequal lobes divided by angular or gibbous to U-shaped sinus descending to $1/5$ -- $1/3$ x leaf length, additional teeth frequently present near leaf base; lobes entire, acute, triangular; cells of midleaf 4-polygonal, 23--28 x 21--25 μ m; cuticle smooth, walls thin to slightly thickened, trigones concave to nearly absent; oil bodies numerous, 10--42 per cell, small, spheric, 2--4.5 μ m in diameter, finely papillose; underleaves present, lanceolate, 2-lobed into 2 narrow lamina or reduced to slime papilla. **Specialized asexual reproduction** absent. **Sexual condition** paroicous. **Androecia** intercalary, male bracts 2--3(--4) pairs, similar to leaves but inflated in the base, additional tooth near antical base commonly present, 1-androus, antheridial stalk 1-seriate. **Gynoecia** terminal, female bracts in 1 pair, oval to ovoid, deeply (2--3)-lobed, nearly entire, but sometimes with additional teeth, ca. 0.6 x 0.6 mm, divided to $1/4$ -- $2/5$ x length into (2--3) lobes, bracteole present, deeply 2-lobate, ca. 0.5--0.2 mm connate with bracts to $1/2$ x length. **Perianth** exerted to $3/4$ x length, obovate-clavate to cylindric, complicated at mouth, mouth denticulate to dentate with 1--2-celled teeth, generally 1-stratose. **Elaters** ca. 6 μ m thick. **Spores** 10--14 μ m in diameter.

Permanently damp peaty slopes, wet moss mats in moist tundra, among or over mosses and other liverworts in dense patches; elevation unknown; Greenland; Alta.; n Eurasia.

XXe. LOPHOZIA subg. **OBTUSIFOLIUM** (H. Buch) Bakalin

Barbilophozia subg. *Obtusifolium* H. Buch, Mem Soc. F. Fl. Fenn. 17: 289. 1942

Plants ca. 20--50 x 2--3.5 mm, prostrate, greenish brown, brownish to brownish yellow, rarely with purple tinge or dark green in shady places. **Stems** 0.3--0.5 mm in diameter, sparsely branching, transverse section commonly without microcellous layer, but sometimes with exception of 2--3 layers of cells smaller than inner ones, outer cells in stem cross section thin; ventral side of the stem nearly the same color with the dorsal. **Leaves** subhorizontally inserted, more or less distant, spreading, flattened, 2(--3)-lobed, cells with many (to 50 per cell) small, spheric oil-bodies; cuticle distinctly papillose; underleaves commonly absent, rarely present, ciliate or lacinulate, 4 cells in length and 1--2(--3) cells wide, easily deciduous. **Specialized asexual reproduction** by angular gemmae, those rarely present, green, with moderate thickened

angles. **Sexual condition** dioicous. **Capsule** oval, walls (4--5)-stratose. **Spores** spheric, 11--14 μm .

Species 1 (1 in the flora): North America, Europe, Asia, Africa.

24. Lophozia obtusa (Lindberg) A. Evans, Proc. Washington Acad. Sci. 2: 303. 1900

Jungermannia obtusa Lindberg, Musci Scand., 7. 1879; *Leiocolea obtusa* (Lindberg) H. Buch, *Obtusifolium obtusum* (Lindberg) S. W. Arnell, *Schistochilopsis obtusa* (Lindb.) Potemkin

Plants ca. 20--50 x 2--3.5 mm, prostrate or epiphyte on sedges or other boggy grasses, greenish brown, brownish to brownish yellow, rarely with purple tinge or dark green (in shady places). **Stems** 0.3--0.45 mm diameter, sometimes transversely oval in transverse section (ca. 0.25 mm in height), sparsely branching, transverse section commonly without microcellous layer, but occasionally with 2--3 layers of cells smaller than inner ones located above ventral cortex, ventral surface brown to reddish brown; rhizoids common sometimes dense, in indistinct fascicles, colorless to yellowish and brownish. **Leaves** commonly very obliquely inserted to nearly horizontally, insertion line nearly straight, distant, spreading, flattened, lingulate to orbicular, 1--1.2 x 1.2--1.4 mm, 2-lobed, subequal lobes divided by gibbous sinus descending to $1/5$ (-- $1/4$)x leaf length; lobes entire, rounded to obtuse; cells of midleaf 4--polygonal, 32--38 x 21--25 μm , in base to 50 x 38 μm ; cuticle almost always distinctly striolate papillose through, especially obvious at the base, walls thin, trigones concave to triangular; oil bodies minute, 15--50 per cell, spheric, 2--3 μm in diameter, nearly smooth; underleaves commonly absent, rarely present, ciliate or lacinulate, 4 cells in length and 1--2(--3) cells wide, easily deciduous. **Specialized asexual reproduction** by gemmae at shoot apices, rarely present, pale green to brownish, commonly with 4--5-angular in outline, 17--22 x 17--20 μm , 2-celled, with slightly thickened angles. **Sexual condition** dioicous. **Androecia** intercalary, male bracts 6--12 pairs, spicate, 2--3-androus, antheridial stalk 1-seriate. **Gynoecia** terminal, innovations absent, female bracts in 1 pair, oval to ovoid, 2--4-lobed, entire, ca. 1.1 x 1 mm, divided to $1/7$ -- $1/5$ x length, bracteole present, 2-lobed. **Perianth** exerted to $3/4$ x length, cylindrical, ellipsoidal to clavate, complicated at mouth, mouth denticulate to dentate. **Seta** ca. 3--5 mm, capsule oval, wall 5-stratose, exterior wall with nodular thickenings, interior walls with annular thickenings, reddish brown. **Elaters** ca. 7--9 μm wide. **Spores** ca. 11--14 μm in diameter.

Isolated stems (never in pure mats) among mosses, wet meadows, green-moss bogs, sometimes on moist slopes or waterways; 0--2150 m; Greenland; Alta., B.C., Nfld. and Labr. (Nfld.), N.W.T., Nunavut, Que., Yukon; Alaska, Ariz., Calif., Colo., Idaho, Maine, Mich., Mont., Oreg., Wash., Wyo.

6. GYMNOCOLEA (Dumortier) Dumortier, Recueil Observ. Jungerm., 17. 1835 * [Greek, *gymno*-, naked and *koleo*-, female sheath, alluding to the large perianth, not concealed by bracts]

Marie L. Hicks
Richard H. Zander

Jungermannia sect. *Gymnocolea* Dumortier, Syll. Jungerm. Eur., 52. 1831

Plants creeping with ascending apices, mat forming or erect when crowded, green to blackish

brown or scorched in insolated sites. **Stems** 7--8 cells in diameter, branching terminal, lateral or ventral intercalary, from older stems, cortical cells thin-walled, 20--25 μm , little differentiated from medullary; rhizoids sparse, scattered along ventral stem or restricted to area of ventral leaf base, colorless. **Leaves** succubous-oblique, 2-lobed, the lobes obtuse to rounded, occasionally acute, often concave; leaf cells subisodiametric, small, 22--30 μm ; cuticle smooth, occasionally slightly verruculose or striolate; walls without distinct trigones or small, not bulging; oil bodies smooth to slightly granulate. **Underleaves** absent or occasional and small, of 1--4 cells from narrow ventral merophytes of 2--4 cells. **Specialized asexual propagation** sometimes by detached inflated perianths that float on water; gemmae absent or very rare, angular, brown, 1--2 celled. **Sexual condition** dioicious. **Androecia** terminal, spicate, becoming intercalary, of ventricose bracts similar to leaves but smaller; antheridia one per bract; stalk 1-seriate. **Gynoecea** terminal on main stem or branch, often with subfloral innovations; bracts similar to leaves; bracteole absent; perianth exerted, inflated, smooth, the mouth contracted or not; perigynium absent. **Sporophyte** seta cross section of 8 exterior cells and 4 interior cells; capsule ovoid, brown, valves 2 cells thick, the walls with nodular thickenings; elaters 120--200 \times 6--9 μm , 2-spiral, brown. **Spores** 10--18 μm , finely papillose, brown.

Species 6 (4 in the flora); temperate areas of the Northern Hemisphere and South America.

SELECTED REFERENCES Schuster, R. M. 1969. The Hepaticae and Anthocerotae of North America, Vol. II. New York.

1. Rhizoids restricted to area of ventral leaf base ... 4. *Gymnocolea fasciniifera*
1. Rhizoids few or absent, scattered over ventral stem.
 2. Leaf lobes with obtuse or rounded apices . . . 1. *Gymnocolea inflata*
 2. Leaf lobes with acute or obtusely acute apices.
 3. Leaves 370--600 μm , 2-lobed to 1/3--1/2; perianths sharply contracted at mouth . . . 2. *Gymnocolea acutiloba*
 3. Leaves 840--1230 μm , 2-lobed to 1/3; perianths not sharply contracted at mouth ... 3. *Gymnocolea borealis*

1. *Gymnocolea inflata* (Hudson) Dumortier, Recueil Observ. Jungerm., 17. 1835

Jungermannia inflata Hudson, Fl. Angl. ed. 2. 2: 511. 1778

Plants with shoots 5--25 \times 0.75--1.2 mm, scattered among mosses or in crowded mats, green in shade or brownish-black in exposed sites. **Stems** slender, 130--300 μm , branching irregular, terminal or ventral intercalary. **Rhizoids** sparse, scattered ventrally on stem. **Leaves** distant to scarcely imbricate, spreading, flat or more often concave, as long as wide or slightly longer, 400--900 \times 350--800 μm , 2-lobed 1/4--1/3, the sinus narrow, the lobes obtuse to rounded, entire; median leaf cells 22--27 \times 25--30 μm , marginal cells 20--24 μm ; cuticle smooth, walls evenly thickened; trigones absent; oil bodies 4--8 per cell, ovoid or spheric, 3--4 \times 5--6 μm , finely granulate. **Underleaves** absent. **Specialized asexual propagation** by detached, unfertilized, inflated perianths that float on water, gemmae absent. **Androecial** bracts up to 8 pairs, contiguous, concave, 2-lobed. **Gynoecea** commonly with subfloral innovations; bracts similar to leaves in

shape, slightly larger; perianths often present, exerted well above bracts, globose to oblong, inflated, large compared to the size of the shoot, mouth contracted, dentate-lobulate; easily detached from stem.

Igneous rock outcrops subject to at least periodic seepage, often in direct sunlight; also around rock pools and in bogs; e, w, nw Greenland; Miquelon; Alta., Ark., B.C., Man., Nfld., N.S., Nun., Ont., Que., Yukon; Alaska, Calif., Colo., Conn., Maine, Mass., Mich., Minn., N. C., N.H., N.J., N.Y., Oreg., Pa., S.Dak., Tenn., Vt., Wash., Wyo.; Europe; Asia (Japan).

The variety *Gymnocolea inflata* var. *heterostipa* (Carrington & Spruce) K. Müller, characterized with frequent small intercalary branches and small underleaves, has been recognized from plants collected in East Greenland and Minnesota. This plant is doubtfully distinct and its gametophytic differences may be an environmentally induced variation. In Europe, where the variety was first recognized, no distinct limits have been found between this variety and the typical form of *Gymnocolea inflata*.

2. *Gymnocolea acutiloba* (Schiffner) Müller Frib., Lebermoose 1(12): 745. 1910

Lophozia inflata var. *acutiloba* Schiffner, Sitzungsber. Deutsch. Naturwiss.-Med. Vereins Böhmen "Lotos" Prag 53: 111. 1905; *Gymnocolea inflata* subsp. *acutiloba* (Schiffn.) R. M. Schust. & Damsh. ex L. Söderstr. & Vána

Plants with shoots 10--15 × 0.6--0.9 mm, forming mats, green to brown or blackish. **Stems** 100--180 μm, sparingly branched, the branches terminal, occasionally intercalary. **Rhizoids** sparse, scattered ventrally on stem. **Leaves** remote to slightly overlapping, nearly flat, ovate-quadrate, slightly longer than wide, 370--600 × 320--500 μm, 2-lobed 1/3--1/2, with a narrow sinus and subacute to acute lobes ending in 1--2 cells; lateral leaf margins often with a small tooth; leaf cells subquadrate, 22--28 μm, walls slightly thickened, often brownish; trigones not developed; oil bodies 3--8 per cell, ovoid or spherical 4--6 × 5--8 μm, smooth or slightly granular. **Underleaves** absent or vestigial, of small cilia or slime papillae. **Specialized asexual propagation** usually absent or rarely by gemmae on margins of leaf lobes, angular, 14--18 μm, 2-celled, brown, plants usually sterile. **Gynoecea** with bracts similar to leaves in shape, larger; perianth rarely produced, inflated, clavate, the mouth sharply contracted, dentate.

Igneous rock that are perhaps copper-bearing, where they may occur with other rare species such as *Cephaloziella massalongoi* or *Gymnomitrium concinatum*; w Greenland; Alaska, Maine, Tenn.; Europe.

The perianths of *Gymnocolea acutiloba* are characteristically not easily detached,

3. *Gymnocolea borealis* (Frisvoll & Moen) R. M. Schuster, Lindbergia 12: 7. 1986

Lophozia borealis Frisvoll & Moen, Lindbergia 6: 138. fig. 1--3, 1980

Plants with shoots 10--30 × 0.5--2.5 mm, scattered among mosses, golden-brown. **Stems** 150--200 μm, simple or pseudodichotomously branched, the branches of *Frullania*-type. **Rhizoids** few or nearly absent, scattered ventrally on stem. **Leaves** remote or rarely slightly overlapping, nearly

flat to dorsally convex, ovate-quadrate, slightly longer than wide, 840--1230 x 740--1060 μm , 2-lobed to 1/3, occasionally 3--4-lobed, with a narrow sinus and subacute to acute lobes ending in a 1--2-celled mucro; lateral leaf margins repand to crenulate; leaf cells rounded-polygonal, 22--28 x 24--30 μm , walls moderately thickened; trigones small, never bulging; oil bodies 1--5(--8) per cell, ovoid, ellipsoidal or spherical, 4--8 x 4--10 μm , finely granulate. **Underleaves** present, of 1--3(--4) uniseriate cells ending in a slime papilla. **Specialized asexual propagation** absent. **Gynoecia** with bracts 2--4-lobed, variable in size; perianth elongate-obovate to pyriform, weakly 3--4-plicate distally, mouth plicate, lobulate, dentate, not sharply contracted.

Rich fens, swamps, rock depressions in seepage, irrigated low swale, interspersed among mosses; low to moderate elevations; nw and w Greenland; Nunavut (Baffin I.); Europe (Finland, Norway, Sweden).

Gymnocolea borealis occurs as scattered among mosses, golden-brown, the leaves are distant, usually dorsally convex and horizontally arranged, leaf lobes obtuse to acute, the oil bodies are relatively large, leaf cuticle is striate-verruculose, and underleaves are evident because the rhizoids are few or absent.

4. *Gymnocolea fascinifera* Potemkin, Arctoa 2: 76, fig. 5--6. 1993

Plants with shoots 5--15 x 1--2.5 mm, scattered among mosses, green to brown, matte. **Stems** slender, 130--200 μm , branching often terminally furcate, rarely ventral and lateral intercalary. **Rhizoids** restricted to area of ventral leaf base. **Leaves** distant, spreading, flat, as long as wide or to twice as long, 700--1000 x 350--650 μm , 2-lobed 1/4--1/3, asymmetric, the sinus broad, the lobes obtusely acute to rounded-apiculate, entire; median leaf cells 20--45 x 20--35 μm , marginal cells 17--30 μm , walls thin; trigones small to bulging; oil bodies 4--8 per cell, ovoid or spherical, 3--4 x 5--6 μm , finely granulate. **Underleaves** small, of 2 stalked slime papillae, or absent. **Specialized asexual propagation** absent. **Androecial bracts** 1--2-androus, contiguous, concave, 2-lobed, the antical small. **Gynoecia** unknown.

Arctic tundra, soil; low to moderate elevations; Alaska; Asia (Siberia).

Gymnocolea fascinifera has been collection once in the flora region: Alaska, Seward Peninsula, south Killeak Lake, in well developed troughs of high centered polygon. The cell wall cuticle is smooth or more often striolate, It differs from congeners by the rhizoids restricted to the area of the ventral leaf base. From *G. inflata*, it differs in more numerous oil bodies, yellowish brown color, leaves with differently sized and apiculate lobes.

7. ANASTREPTA (Lindberg) Schiffner, Hepat. in A. Engler & G. Prantl, Nat. Pflanzenfam. 1(3): 85. 1893 * [Greek *ana-*, throughout, and *strept-*, turn, alluding to leaf tips facing the same direction]

Jungermannia sect. *Anastrepta* Lindberg in Lindberg & Arnell, Kongl. Svenska Vetensk.. Handl., n.s. 23(5): 40. 1889

Dale H. Vitt

Plants ca 2--8(--12) cm long, 0.6--3.5 mm wide, reclining to erect. **Stem** transverse section with 3--4 cortical cell layers and 15--25 medullary cells; rhizoids short, colorless to pale brown.

Leaves succubous, subtransversely-obliquely inserted, often strongly asymmetric, weakly and usually unequally 2-lobed, sinus obsolete or to 1/6 leaf length or less, often unlobed, asymmetric; cells with thin or somewhat thickened walls, trigones small to large and convex; oil bodies 3--16 per cell, homogeneous or faintly granular; underleaves absent. **Sexual condition** dioicous.

Specialized asexual reproduction by angular gemmae. **Androecia** apical becoming intercalary with age, antheridial stalk 2-seriate, female bracts leaf-like, undulate and somewhat crisped, 2--5-lobed, bracteoles 1--2-lobed. **Perianth** ellipsoidal to obovoid, suddenly narrowed to a dentate-ciliate mouth. **Sporophytes** unknown in flora area.

Species 1 (1 in the flora): widely scattered in oceanic and mountainous areas, nw N. Amer. Europe, Asia, Pacific Ocean Islands (Hawaii).

SELECTED REFERENCES: Paton, J. A. 1999. The Liverwort Flora of the British Isles. Harley Books, Essex, England.

1. **Anastrepta orcadensis** (Hooker) Schiffner, Hepat. in A. Engler & G. Prantl, Nat. Pflanzenfam. 1(3): 85. 1893

Jungermannia orcadensis Hooker, Brit. Jungermann, pl. 71. 1815

Plants loose, slender, unbranched, growing among other bryophytes, dull green to olive-green to reddish brown. **Leaves** shallowly notched, erect to squarrose and reflexed toward to the ventral side of the shoot, about 1.8 mm long and wide, concave at base, otherwise plane or antically recurved, leaf cells 18--23 /um wide.

Among other bryophytes on peaty banks and humus on and around cliffs; sea level to subalpine; B.C.; Alaska; Europe; Asia (China, Japan, Russia).

The very shallowly 2-lobed, convex leaves are characteristic of *Anastrepta orcadensis*. Additionally, the postical portion of the leaves is strongly recurved, and there are no underleaves.

8. SCHISTOCHILOPSIS (N. Kitagawa) Konstantinova in Konstantinova & Vasiljev, Arctoa 3: 125. 1994 * [Genus *Schistochila*, and Greek *opsis*, similar, alluding to characteristic presence of winged keel in one species]

Vadim Bakalin

Lophozia subg. *Schistochilopsis* N. Kitagawa, J. Hattori Bot. Lab. 28: 289. 1965; *Heterogemma* (Jørg.) Konstant. & Vilnet, *Massula* K. Müller ex Schljakov, *Trilophozia* (R. M. Schuster) Bakalin

Plants ca. 10--50 x 1--3 mm, prostrate to ascending, from pale green to bright green and slightly brownish. **Stems** transversely oval, soft-textured, 0.4--1.1 mm in width and 0.4--0.6 mm in

height, sparsely branching, stem in transverse section composed by homogenous cells, outer cells not different, ventral side of the stem differing in color or concolorous with dorsal side; rhizoids sparse to common, in indistinct fascicles, colorless to pale brownish. **Leaves** succubous, inserted at various angles, distant to imbricate, spreading to appressed, flat to concave, divided by variously shaped sinus into 2--3(--4) lobes; lobes toothed or entire; cells collenchymatous or not, walls usually thin, but sometimes thickened; oil bodies 5--50 per cell, biconcentric or otherwise; underleaves usually absent. **Specialized asexual reproduction** by gemmae in masses at apices of shoots or on tips of specialized, attenuate branches. **Sexual condition** dioicous. **Androecia** intercalary, 2--5-androus, antheridial stalk (1--2)-seriate. **Gynoecia** terminal, female bracts in 1 pair. **Perianth** exerted $1/2--3/4$ its length, mainly cylindric, complicated at mouth, mouth dentate to ciliate and lobulate; perigynium entirely absent. **Capsule** oval, walls (3--5)-stratose, exterior walls with nodular thickenings, interior walls with annular thickenings, reddish brown. **Elaters** 2-spiral, reddish brown. **Spores** 10--16 μ m.

Species 8 (5 in the flora): North America, South America, Eurasia, n Africa.

SELECTED REFERENCES: Schuster R.M. 1969. The Hepaticae and Anthocerotae of North America. New York and London. Vol. 2. Bisang, J. 1991. Biosystematische studien on *Lophozia* subg. *Schistochilopsis* (Hepaticae). Bryophytorum Bibl. 43. Berlin-Stuttgart. 187 pp., 17 plates.

Species 6 (3 in the flora): North America, South America, Eurasia, n Africa.

1. Stems commonly wider 0.5 mm; leaves of sterile shoots commonly 2--3-lobed; gemmae sharply angled . . . XXa. *Schistochilopsis* sect. *Schistochilopsis*

1. Stems commonly lesser 0.4 mm wide; leaves of sterile shoots predominantly 2-lobed; gemmae ellipsoidal . . . XXb. *Schistochilopsis* sect. *Heterogemmae*

XXa SCHISTOCHILOPSIS (N. Kitagawa) Konstantinova sect. SCHISTOCHILOPSIS

Lophozia sect. *Incisae* R. M. Schuster

Plants ca. 5--50 x 1.2--2.5 mm, pale whitish green to bright green and brownish at distal apices.

Stems commonly wider than 0.5 mm. **Leaves** 2--3(--4)-lobed with acute lobes ending in a protruding and elongate cell. **Specialized asexual reproduction** by sharply angled gemmae.

1. Stem ventrally blackish purple; leaf margins mostly entire . . . 1. *Schistochilopsis grandiretis*

1. Stem ventrally dirty green to blackish, lacking purplish pigmentation; leaf margins mostly dentate.

2. Plants deep green with brownish lobes near apex, stem in old parts of shoot ventrally blackish; oil-bodies 5--20 per cell, papillose, non-biconcentric . . . 2. *Schistochilopsis hyperarctica*

2. Plants light green to bluish green, lobes near apex green, sometimes decolorate, never brownish, stem in old parts of shoot ventrally not becoming blackish; oil-bodies 15--50 per cell, nearly homogenous, sometimes biconcentric . . . 3. *Schistochilopsis. incisa*

1. *Schistochilopsis grandiretis* (Lindberg ex Kaalaas) Konstantinova, *Arctoa* 3: 125. 1994

Jungermannia grandiretis Lindberg ex Kaalaas, *Nyt Mag. Naturvidensk.* 33: 322. 1893;
Lophozia grandiretis (Lindberg ex Kaalaas) Schiffner, *Lophozia grandiretis* var. *parviretis* R. M. Schuster

Plants ca. 20--50 x 1.2--2.4 mm, prostrate, pale green to greenish, sometimes with brownish colored tips. **Stems** transversely oval in cross section, soft-textured, 0.4--0.8 mm in width and 0.4--0.5 mm in height, sparsely branching, transverse section without microcellous layer, ventral side vinaceous to purplish brown and purplish black; rhizoids common, sometimes dense, in indistinct fascicles, colorless to yellowish and brownish. **Leaves** commonly obliquely inserted to nearly subtransverse, insertion line nearly straight, distant, spreading, flattened to undulate and crispate, transversely oval, 1.2--1.4 x 1.5--2 mm, 2--3-lobed, unequal lobes divided by gibbous sinus descending to $1/5$ -- $2/5$ leaf length; lobes weakly dentate, acute, frequently with some teeth near apex; cells of midleaf 4-polygonal, 38--75 x 35--50 μm , in base up to 55 x 95 μm ; cuticle smooth, walls very thin, trigones concave to triangled; oil bodies 15--50 per cell, spherical, 4--5 μm in diameter, nearly homogenous; underleaves absent. **Specialized asexual reproduction** by gemmae at apices of shoot, pale green, commonly with 4--6-angled in projection, 24--36 x 20--27 μm , 2-celled, with sharply protruding angles. **Sexual condition** dioicous. **Androecia** intercalary, male bracts in 3--5 pairs, spicate, 3--5-anded, antheridial stalk 2-seriate. **Gynoeceia** terminal, innovations absent, female bracts in 1 pair, oval to ovoid, 2--4-lobed, sharply to weakly dentate, ca. 1.5 x 2.2 mm, divided to $1/4$ -- $1/3$ their length, bracteole present, 2-fid. **Perianth** exerted to $1/2$ its length, cylindric to cone-shaped, complicated at mouth, mouth denticulate to subentire. **Elaters** ca. 10--12 μm wide. **Spores** ca. 15--18 μm .

Usually peat or over *Sphagnum* in peat moss bogs, wet slopes of waterways, opened coniferous forest, very rarely sandy soil in tundra; elevation unknown; Greenland; Alta., Man., N.W.T., Que., Yukon; Alaska, Minn., Vt., Wash.; n Eurasia.

The typical form of *Schistochilopsis grandiretis* is apparently limited to Greenland and Nunavut (Ellesmere I.). The remainder of material in the range of the flora is properly referred to *S. grandiretis* subsp. *proteidea* (Arnell) Stotler & Croand.-Stotl. (R. Stotler and B. Crandall-Stotler 2017).

2. *Schistochilopsis hyperarctica* (R. M. Schuster) Konstantinova, *Arctoa* 3: 125. 1994

Lophozia hyperarctica R. M. Schuster, *Canad. J. Bot.* 39: 967. 1961

Plants ca. 5--12 x 1.5--1.8 mm, prostrate, pale green to greenish, sometimes with characteristic brownish ends of lobes near apex. **Stems** transversely oval in cross section, soft-textured, 0.4--1.1 mm in width and 0.3--0.5 mm in height, sparsely branching, transverse section without microcellous layer, ventral side of stem dirty green to blackish, with no trace of purplish

pigmentation; rhizoids common, sometimes dense, in indistinct fascicles, colorless to yellowish and brownish. **Leaves** commonly obliquely inserted to nearly subtransverse, insertion line nearly straight, distant, spreading, flattened to undulate and crispate, transversely oval, 1.2--1.4 x 1.5--2 mm, 2--4-lobed, unequal lobes divided by gibbous sinus descending to $1/5$ -- $2/5$ leaf length; lobes weakly to sharply dentate, acute, frequently with some teeth near apex; cells of midleaf 4--polygonal, ca. 35--50 x 35--45 μm , in base up to 45 x 50 μm ; cuticle smooth, walls very thin, trigones concave to triangled; oil bodies 5--20 per cell, ellipsoidal; underleaves absent.

Specialized asexual reproduction by gemmae at shoot apices, pale green, commonly 4--6-angled in outline, 24--36 x 20--27 μm , 2-celled, with sharply protruding angles. Otherwise unknown.

Acid to basic wet tundra communities, over *Sphagnum* or mosses, rarely mineral soil; elevation unknown; Nunavut; Alaska; n Eurasia.

3. *Schistochilopsis incisa* (Schrader) Konstantinova, Arctoa 3: 125. 1994

Jungermannia incisa Schrader, Syst. Samml. Krypt. Gew. (2): 5. 1797; *Lophozia incisa* (Schrader) Dumortier

Plants ca. 5--25 x 1.2--2.5 mm, prostrate, pale green to greenish, bluish green and deep green. **Stems** transversely oval in cross section, soft-textured, 0.4--0.9 mm in width and 0.4--0.5 mm in height, sparsely branching, transverse section without microcellous layer, ventral side of stem dirty green to brownish green, with no trace of purplish pigmentation; rhizoids common, sometimes dense, in indistinct fascicles, colorless to yellowish and brownish. **Leaves** commonly obliquely inserted to nearly subtransverse, insertion line nearly straight, distant, spreading, flattened to undulate and crispate, transversely oval to obtuse, 1--1.7 x 1.7--2.2 mm, 2--4-lobed, unequal lobes divided by gibbous sinus descending to $1/5$ -- $2/5$ leaf length; lobes weakly to sharply dentate, acute, frequently with some additional teeth near apex; cells of midleaf 4--polygonal, ca. 30--45 x 25--32 μm , in base up to 45 x 50 μm ; cuticle smooth, walls very thin, trigones concave to triangled, rarely convex; oil bodies 15--45 per cell, spherical, 4--5 μm in diameter, nearly homogenous, sometimes biconcentric; underleaves absent. **Specialized asexual reproduction** by gemmae at shoot apices, pale green, commonly 4--6-angled in outline, 24--36 x 20--27 μm , 1--2-celled, with sharply protruding angles. **Sexual condition** dioicous. **Androecia** intercalary, male bracts 3--5 pairs, spicate, 3--5-anded, antheridial stalk 2-seriate. **Gynoecia** terminal, innovations absent, female bracts in 1 pair, oval to ovoid, 2--4-lobed, sharply to weakly dentate, ca. 1.5 x 2.2 mm, divided to $1/4$ -- $1/3$ their length, bracteole present, 2--3-fid. **Perianth** exerted to $1/2$ its length, cylindric to cone-shaped, complicated at mouth, mouth ciliate-dentate with teeth usually 1--3(--4) cells long. **Seta** ca. 3--5 mm, capsule oval, walls 5-stratose, exterior walls with nodular thickenings, interior walls with annular thickenings, reddish brown. **Elaters** ca. 7--10 μm wide. **Spores** (10--)12--15 μm .

Varieties 2 (2 in the flora): North America; Central America; Eurasia.

1. Leaf cells 1--2-stratose at base, terminal cell of antical leaf lobe 3--4x long as wide, plants bright green; mainly forest communities, predominantly decaying wood . . . 3a. *Schistochilopsis incisa* var. *incisa*

1. Leaf cells in 2--3(--4) layers in the proximal third of leaf; terminal cell of antical leaf lobe 1.2--1.7(--2)\x wide as long, plants pallid; predominantly tundra belt or latitudinal zone . . . 3b.

Schistochilopsis incisa var. *opacifolia*

3a. *Schistochilopsis incisa* (Schrader) Konstantinova var. **incisa**

Plants bright green. **Leaves** sharply spinose-dentate, 1--2-stratose at base; terminal cell in antical leaf lobe ca. 3--4\x long as wide.

Wet, more or less shady habitats, decaying wood, soil, among and over mosses in tundra and forest floor, bogs, slopes, over moss mats; 0--3000 m; Greenland; Alta., B.C., N.B., Nfld. and Labr., N.W.T., N.S., Ont., Que., Yukon; Alaska, Calif., Colo., Conn., Idaho, Ill., Ky., Maine, Mass., Mich., Mont., Nev., N.Mex., N.Y., N.C., Ohio, Oreg., Pa., R.I., Tenn., Utah, Vt., Va., Wash., W.Va., Wis., Wyo.; Eurasia; Central America.

A minor variant is *Schistochilopsis incisa* var. *inermis* (Müller Frib.) Konstantinova. It is known from Maine, Michigan, and Minnesota, with additional range in Europe. It is distinguished from var. *incisa* by leaves with bulging trigones, leaves unequally bifid, and often nearly transversely inserted

3b. *Schistochilopsis incisa* var. **opacifolia** (Culmann ex Meylan) Bakalin

Lophozia opacifolia Culmann ex Meylan, Rev. Bryol., 47: 21. 1920; *Schistochilopsis opacifolia* (Culmann) Konstantinova; *Lophozia incisa* ssp. *opacifolia* (Culmann) R. M. Schuster & Damsholt

Plants pallid. **Leaves** weakly dentate, 2--3(--4)-stratose at base, terminal cell of antical leaf lobe 1.2--1.7(--2)\x long as wide.

Mainly tundra zone, rarely forest zone as descended from mountain tundra belt, frequently on moist soil in snow-bed communities and rock crevices, in *Sphagnum* bogs, wet moss tundra; rarely wet cliffs in forests; 0--3500 m; Greenland; Alta., B.C., Nfld. and Labr. (Nfld), N.W.T., Nunavut, Yukon; Alaska, Calif., Colo., Mont., Oreg., Utah, Wash.; North Eurasia.

XXb SCHISTOCHILOPSIS sect. HETEROGEMMAE (Jørgensen) Bakalin, Bryologist 114: 313. 2011

Lophozia sect. *Heterogemmae* Jørgensen, Bergens Mus. Skr. s.n. 16: 1959. 1934; *Lophozia* sect. *Marchicae* R. M. Schuster

Plants ca. 10--20 x 1--2 mm, pale green-whitish to nearly white. Stems commonly less than 0.4 mm wide. **Leaves** 2--(3--4)-lobed with obtuse to rounded lobes not ending by a protruding, elongate cell. **Specialized asexual reproduction** by ellipsoidal gemmae.

Species 2 (2 in the flora): North America, n Eurasia.

1. Stem ventrally purplish-black; plants of bogs . . . 5. *Schistochilopsis laxa*

1. Stem ventrally same color as dorsally or slightly brownish; plants of mineral soil . . . 4.
Schistochilopsis capitata

4. *Schistochilopsis capitata* (Hooker) Konstantinova, *Arctoa* 3: 125. 1994

Jungermannia capitata Hooker, *Brit. Jungerm.*, tab. 80. 1816; *Lophozia capitata* (Hooker) Macoun; *Heterogemma capitata* (Hook.) Konstant. & Vilnet; *Tritomaria capitata* (Hooker) Stotler & Crandall-Stotler

Plants ca. 10--20 x (1--1.3--1.5(--2) mm with gemmiparous attenuate shoots 0.2--0.5 mm in width, prostrate, pale green to greenish and whitish. **Stems** transversely oval in cross section, soft-textured, (0.1--0.15--0.25(--0.35) mm in width and ca. 0.15--0.20 mm in height, sparsely branching, transverse section without microcellous layer, ventral side of stem not differing in color from dorsal, with no trace of purplish pigmentation; rhizoids common, sometimes dense, in indistinct fascicles, colorless. **Leaves** commonly obliquely to nearly horizontally inserted, insertion line nearly straight, distant, spreading, flattened to undulate and crispate, transversely oval to obtapezoidal, 0.9--1 x 0.8--1 mm, 2(--3)-lobed, unequal lobes divided by gibbous or angled sinus descending to $1/3--2/5$ leaf length; lobes weakly to sharply dentate, acute, frequently with some additional teeth near apex; cells of midleaf 5--polygonal, ca. 38--45 x 30--38 μm , in base up to 45 x 50 μm ; cuticle smooth, walls very thin, trigones indistinct; oil bodies 15--50 per cell, spherical, 2.4--5.4 μm , to oval, ca. 5 x 6--7 μm , nearly homogenous; underleaves absent or very rarely large, lanceolate, the same length as leaf. **Specialized asexual reproduction** by gemmae at apices of attenuate and thin shoots, pale green to colorless, in exposed places sometimes with rose or purplish coloration, ellipsoidal with papilla near end, 21--28 x 20--24 μm , 1-celled. **Sexual condition** dioicous. **Androecia** intercalary, often violet tinged, male bracts 3--5 pairs, spicate, 1--2-androus, antheridial stalk 1--2-seriate. **Gynoecia** terminal, innovations absent, female bracts in 1--2 pairs, oval to ovoid, 2--3(--3)-lobed, entire or weakly dentate, ca. 1.7--1.9 x 2--3 mm, divided to $1/4--1/3$ their length, bracteole present, 2-fid. **Perianth** exerted to $4/5$ its length, cylindric, complicated at mouth, mouth ciliate-dentate to lobulate with teeth usually 1--3(--4) cells in length, but sometimes up to 5--10 cells in length. **Seta** 5--15 mm. **Capsule** oval, walls 3--5-stratose, exterior walls with nodular thickenings, interior walls with annular thickenings, reddish brown. **Elaters** ca. 7--10 μm wide. **Spores** ca. 12--15 μm .

Predominantly sandy soil, river slopes, roadsides, other native and anthropogenic areas with disturbed vegetation cover, also pure peat, forested area, also tundra; 10--1500 m; Alta., B.C., Nfld. and Labr. (Nfld.), N.S., Ont.; Alaska, Conn., Del., Fla., Iowa, Maine, Mass., Mich., Minn., N.H., N.J., N.Y., N.C., Ohio, Pa., R.I., S.C., Vt., Wash., W.Va.; Europe.

5. *Schistochilopsis laxa* (Lindberg) Konstantinova, *Arctoa*, 3: 125. 1994

Jungermannia laxa Lindberg, Hep. Hibernia, 529. 1875; *Lophozia laxa* (Lindberg) Grolle, *Lophozia novae-caeseriae* Evans, *Heterogemma laxa* (Lindberg) Konstant. & Vilnet, *Tritomaria laxa* (Lindberg) Stotler & Crandall-Stotler

Plants ca. 10--20 x 1.8--2 mm, pale green to greenish and whitish. **Stems** transversely oval in cross section, soft-textured, 0.32--0.5 mm in width and ca. 0.3 mm in height, sparsely branching, transverse section without microcellous layer, ventral side of stem purple to deep violet-blackish; rhizoids sparse to common, in indistinct fascicles, colorless. **Leaves** commonly obliquely to nearly horizontal inserted, insertion line nearly straight, distant, spreading, flattened to undulate and crispate, transversely oval to obtuse, 0.8--1 x 1.1--1.5 mm, 2--3(--4)-lobed, unequal lobes divided by gibbous or angled sinus descending to $1/3--2/5 \times$ leaf length; lobes weakly to sharply dentate, acute, frequently with some additional teeth near apex; cells of midleaf 5--polygonal, ca. 38--45 x 30--38 μm , in base up to 45 x 50 μm ; cuticle smooth, walls very thin, trigones indistinct; oil bodies 30--50 per cell, spherical, 2--4 μm ; underleaves absent or rarely large, lanceolate, the same length as leaf. **Specialized asexual reproduction** by gemmae at apices of attenuate and thin shoots, pale green to colorless, in exposed places sometimes with rose coloration, ellipsoidal with papilla near end, 21--28 x 20--24 μm , 1(--2)-celled. **Sexual condition** dioicous. **Androecia** intercalary, often violet tinged, male bracts 3--5 pairs, spicate, 1--2-androus, antheridial stalk 1--2-seriate. **Gynoeceia** terminal, innovations absent, female bracts in 1--2 pairs, oval to ovoid, 2--3(--3)-lobed, entire or weakly dentate, ca. 1.7--1.9 x 2--3 mm, divided to $1/4--1/3 \times$ their length, bracteole present, 2-fid. **Perianth** exerted to $4/5 \times$ its length, cylindrical, complicated at mouth, mouth ciliate-dentate to lobulate with teeth usually 1--3(4) cells long, but sometimes up to 5--10 cells in length. **Seta** 5--15 mm. **Capsule** oval, walls 3--5-stratose, exterior walls with nodular thickenings, interior walls with annular thickenings, reddish brown. **Elaters** ca. 8 μm wide. **Spores** ca. 13--16(--18) μm .

Usually *Sphagnum* mires, very rarely on *Sphagnum* in open boggy coniferous forest, peat in bog; elevation unknown; B.C., Nfld. and Labr. (Nfld.), N.S., Nunavut, Ont.; Alaska, Conn., Maine, Mass., Mich., Minn., N.H., N.J., N.Y., Oreg., Vt.; Eurasia.

9. ANASTROPHYLLUM (Spruce) Stephani, Hedwigia 32: 139. 1893 * [Greek *ana-*, again, another, *astro-*, star, *phylum*, leaf, alluding to stellate laminal cells]

Jungermannia subgenus *Anastrophyllum* Spruce, J. Bot. 14: 235. 1876; *Crossocalyx* Meylan; *Schizophyllopsis* Váňa & L. Söderström; *Sphenolobus* (Lindberg) Berggren

Curtis R. Björk
Richard H. Zander

Plants small to medium-sized, in loose to dense turfs or mats, prostrate, or more usually ascending, or sub-erect, green, often brownish, reddish or vinaceous. **Stems** branching variously pseudodichotomous (furcate), *Frullania*-type lateral-terminal or lateral- or ventral-intercalary, transverse section with cortex 1--2(--3)-stratose; rhizoids sparse to nearly absent. **Leaves** succubous, cupped, ventral half inserted obliquely and dorsal half transverse, distant to imbricate, spreading to appressed, concave, divided into 2 lobes, sinus shallow to half the length of the leaf; lobes usually vertical and the dorsal folded over the ventral, entire; cells thick-walled

or collenchymatous and trigonous; leaf cuticle usually smooth, occasionally papillose; oil bodies 3--4 or more per cell, size small to moderate, botryoidal. **Underleaves** essentially absent, reduced to slime papillae. **Specialized asexual reproduction** uncommon, by gemmae. **Sexual condition** dioicous, rarely auto- or paroicous. **Androecia** spicate, 1--4-anded, stalk 1--2-seriate. **Gynoecia** terminal, bracts in 1 pair, 2--4-lobed. **Perianth** cylindrical, mouth lobed and ciliate to ciliate-dentate, plicate distally, furrowed dorsally; perigynium absent. **Capsule** ovoid, walls 2--5-stratose, outer wall with nodular thickenings, inner with semilunar bands. **Elaters** 2-spiral. **Spores** 10--15 μm .

Species ca. 30 (9 in the flora); nearly worldwide; concentrated in tropical regions.

In the treatment of their new family Anastrophyllaceae, L. Söderström et al. (2010) split the *Barbilophozia-Orthocaulis* complex into several genera based on molecular data. *Anastrophyllum* itself, however, remained intact, defined as plants erect or ascending, cortical cells of stem less than 2.5 times as long as wide, leaves divided less than half the length, anisophyllous, leaves obliquely inserted on the stem, 2-lobed, lobes of equal size, underleaves reduced or absent, and perianth weakly to distinctly plicate distally.

1. Plants green; branches of similar thickness, terminal and furcate...9. *Anastrophyllum tenue*
1. Plants brownish or reddish; branches usually of different thicknesses, rarely terminal.
 2. Plants on wood; gemmiferous branches numerous, erect, with tightly clasping leaves ...4. *Anastrophyllum hellerianum*
 2. Plants terricolous or saxicolous; gemmiferous branches, if present, not strictly erect and without clasping leaves.
 3. Leaves merely notched at the tip, sinus less than 1/8 leaf length; foliar stems often more than 2 mm wide.
 4. Leaves tapered to the apex, not or scarcely imbricate ...3. *Anastrophyllum donnianum*
 4. Leaves rounded to the apex, imbricate ...1. *Anastrophyllum alpinum*
 3. Leaves conspicuously 2-lobed, sinus more than 1/6 leaf length; foliar stems mostly 0.4--1.6 mm wide.
 5. Leaves 0.3--0.7 mm, attachment nearly transverse throughout the leaf base.
 6. Leaf basal cells more or less quadrate ...6. *Anastrophyllum minutum*
 6. Leaf basal cells mostly elongated, many more than 2x long as wide ...8. *Anastrophyllum sphenoloboides*
 5. Leaves (0.5--)0.7--1.8 mm, attachment transverse in part, curving into an oblique portion.
 - 7 Leaf lobes about equal ...5. *Anastrophyllum michauxii*
 7. Leaf lobes unequal.
 8. Flattened leaves with lobe axes about parallel ...2. *Anastrophyllum assimile*
 8. Flattened leaves with lobe axes divergent ...7. *Anastrophyllum saxicola*

SELECTED REFERENCES Damsholt, K. 2013. The Liverworts of Greenland. Nordic Bryological Society. Long, D. G., J. A. Paton, J. Squirrell, M. Woodhead and P. M. Hollinsworth. 2006. Morphological, ecological and genetic evidence for distinguishing *Anastrophyllum joergensenii* Schiffn. and *A. alpinum* Steph. (Jungermannioptida: Lophoziaaceae). J. Bryol. 28: 108--117. Söderström, L., R. T. De Roo and T. A. J. Hedderon.

2010. Taxonomic novelties resulting from recent reclassification of the Lophoziaceae/Scapaniaceae clade. *Phytotaxa* 3: 47–53.

1. *Anastrophyllum alpinum* Stephani, *Sp. Hepat.* 6: 103. 1917

Plants 4--12 cm x 1--2.5(--3) mm, prostrate or ascending, forming carpets or mats, usually dark red-brown, less often greyish green or olive-brown, glossy. **Stems** 250--400 / μ m thick, branching anisotomic terminal or postical intercalary; rhizoids scarce. **Leaves** anticlinal to longitudinally inserted, postically more or less transversely inserted, imbricate, spreading, moderately to strongly secund, broadly ovate or ovate-elliptic to orbicular, strongly concave, 0.7--2 x 0.6--1.7 mm, longer than to about as long as wide; lobes more or less equal or the antical slightly smaller, sometimes with a weak tooth, sinus 1/5--1/9 long as leaf; central laminal cells 14--19 / μ m, smooth, walls thin, trigones strongly bulging, lumina stellate, oil bodies 2--5(--7) per cell, broadly elliptic to orbicular, botryoid. **Underleaves** absent. **Specialized asexual reproduction** absent, though plants dispersing by fragmentation. **Sexual condition** dioicous. **Androecia** terminal, bracts smaller than the vegetative leaves and less spreading. **Gynoecia** terminal or becoming intercalary, bracts smaller than the vegetative leaves and less spreading or even appressed to perianth; perianths rare and poorly formed. **Sporophytes** not observed.

Tundra bank; 100 m; Alaska (Adak Island, Aleutians); Eurasia (China, Norway, U.K.).

The type of *Anastrophyllum alpinum* is from the Himalayas. It is a rather rare species in its world distribution. D. G. Long et al. (2006) excluded *Anastrophyllum joergensenii* Schiffn. from North America. *Anastrophyllum alpinum* differs from *A. joergensenii* in dark reddish brown color, ventral innovations lacking, and shoots twice as wide as those of *A. joergensenii*.

2. *Anastrophyllum assimile* (Mitten) Stephani, *Hedwigia* 32: 140. 1893
Jungermannia assimilis Mitten, *J. Proc. Linn. Soc.* 5: 93. 1861

Plants 2--5 cm long, (0.75--1)--1.5 mm wide, forming carpets or stems scattered among other bryophytes, medium to dark reddish brown, glossy. **Stems** 150--260 / μ m thick, branching lateral-intercalary or occasionally terminal; ventral surface (and sometimes dorsal) often with colorless or brownish rhizoids. **Leaves** strongly obliquely (ventral half) and transversely (dorsal half) inserted; not or weakly imbricate, spreading, moderately secund, broadly ovate, moderately conduplicate, 0.63--0.84 x 0.7--0.8 mm, mostly slightly longer than wide; lobes deltoid, unequal, the antical one 1/2--2/3 as large, apices acute, sinus V-shaped or somewhat U-shaped, ca. 1/4--1/3 leaf length; central laminal cells 15--22(--25) x 12--17 / μ m to 13--15 / μ m (marginal), smooth, collenchymatous to weakly trigonous, basal cells longitudinally rectangular, slightly sinuous, medial shortly rectangular to elliptic or somewhat stellate; oil bodies 2--6 per cell, elliptic, finely botryoid. **Underleaves** absent. **Specialized asexual reproduction** lacking, or plants dispersing through fragmentation. **Sexual condition** dioicous. **Androecia** becoming intercalary, bracts imbricate, similar to vegetative leaves. **Gynoecia** intercalary, bracts similar to the vegetative leaves but mostly more shallowly lobed or even unlobed, sheathing proximal 1/4 of perianth; perianths slightly to distinctly tapering upward, deeply plicate, mouth whitish, lacerate with shortly ciliate lobes. **Sporophytes** not observed.

On siliceous rock, boulders, occasionally slate, outcrops, cliff face; 0--1600 m; Greenland; Alta., B.C., Nfld. and Labrador (Labrador); N.W.T., Que., Yukon; Alaska, Wash.; Eurasia.

Anastrophyllum assimile is similar to *A. minutum*, but is distinguished by coarse trigones rather than evenly thickened cell walls, the basal laminal cells are elongate, black or brownish black color, and decurrent dorsal leaf margins.

3. *Anastrophyllum donnianum* (Hooker) Stephani, Hedwigia 32: 140. 1893 (as donianum)
Jungermannia donniana Hooker, Brit. Jungermann., pl. 30. 1813

Plants 4--12 cm long, 1--3(--4) mm wide, forming carpets or mats, usually dark red-brown, less often greyish green or olive-brown, glossy. **Stems** (160--250--400 / μ m thick, branching anisotomic terminal or postical intercalary; rhizoids scarce. **Leaves** inserted obliquely to longitudinally (antical) and more or less transversely (postical); not or weakly imbricate, strongly spreading, moderately to strongly secund, ovate, strongly canaliculate, 0.8--1.3(--1.5) x 1--1.8(--2) mm, longer than wide; lobes unequal, the antical smaller, sinus less than 1/8 long as leaf, variable in outline; central laminal cells 14--18 / μ m wide, smooth or papillose, walls thin, trigones strongly bulging, lumina stellate,; oil bodies 2--8 per cell, broadly elliptic to orbicular, botryoid. **Underleaves** absent. **Specialized asexual reproduction** absent, though plants dispersing by fragmentation. **Sexual condition** dioicous. **Androecia** terminal, bracts smaller than the vegetative leaves and less spreading. **Gynoecia** terminal or becoming intercalary, bracts smaller than the vegetative leaves and less spreading or even appressed to perianth; perianths occasional, clavate or cylindric-clavate, plicate nearly to base, mouth concolorous, lacerate with ciliate lobes. **Sporophytes** very rare, not observed.

Alpine terrace, granite outcrop, peaty slope, subalpine bog slope, blanket bog; 0--500 m; B.C.; Alaska; Eurasia.

Anastrophyllum donniacum is a globally rare species.

4. *Anastrophyllum hellerianum* (Nees ex Lindenberg) R. M. Schuster, Amer. Midl. Naturalist 42: 575. 1949

Jungermannia helleriana Nees ex Lindenberg, Syn. Hepat. Eur., 64. 1829; *Crossocalyx hellerianus* (Nees ex Lindenberg) Meylan

Plants 0.2--0.5(--0.8) cm long, 0.15--0.5(--0.8) mm wide, forming short mats or scattered among other bryophytes, olive green to brown, not glossy. **Stems** 100--200 / μ m thick, branching sparse, furcate, and often with gynoeical innovations; ventral surface with colorless rhizoids and often mycorrhizal wefts. **Lateral leaves** not or weakly imbricate, strongly spreading to (on gemmiferous stems) appressed, not or moderately secund, oblong-ovate, weakly to canaliculately conduplicate, 0.28--0.3(--0.35) x 0.26--0.28(--0.36) mm, longer than or as long as wide; insertion transverse; lobes deltoid to ovate-deltoid, about equal, sinus V-shaped, ca. 1/3--2/5 leaf length; central laminal cells 16--25 x 14--18 / μ m to ca. 12--17 / μ m wide (marginal), smooth or cuticle verruculose, not or weakly collenchymatous, basal cells shortly rounded-rectangular, medial shortly rounded-rectangular,; oil bodies (2--3(--4) per cell, elliptic to orbicular, finely granular. **Underleaves** absent. **Specialized asexual reproduction** gemmae always present on slender,

erect, often pallid stems, red to dark red, 1-celled, mostly cubic, 10--12 / μ m. **Sexual condition** dioicous. **Androecia** terminal, sometimes becoming intercalary, bracts imbricate, ventricose, 2-lobed. **Gynoecia** becoming intercalary or terminal on leafy branches, bracts much larger than the vegetative leaves, 2-lobed, lobes dentate to dentate-serrate, spreading from or loosely sheathing the perianth; perianths common, ovate-cylindric, plicate nearly to base, mouth concolorous, lacerate with shortly ciliate lobes. **Sporophytes** occasional; capsule elliptic, wall of 2 or in part 3 cell layers, epidermal and interior wall cells with columnar nodular thickenings. Elaters closely 2-spiral, each 2.5 / μ m wide. Spores granular-vermiculate, 10--12 / μ m.

On wood, rotten log, birch, *Tsuga* bark; 100--1036 m; B.C., N.B., Nfld. and Labrador (Nfld.), N.W.T., N.S., Ont., Que.; Alaska, Conn., Ga., Idaho, Mass., Maine, Mich., Minn., N.H., Tenn., Ver., Wash. Wis., W.Va.; Eurasia.

Anastrophyllum hellerianum and *A. michauxii* are two species in the genus that commonly grow on wood, particularly on old logs. Erect, gemmiferous branches are an important trait for identification of *A. hellerianum*.

5. *Anastrophyllum michauxii* (F. Weber) H. Buch, Memoranda Soc. Fauna Fl. Fenn. 8: 289. 1932

Jungermannia michauxii F. Weber, Hist. Musc. Hepat. Prodr., 76. 1815

Plants 1.5--5 cm long, (1--1.2--2(--2.5) mm wide, forming carpets or mounds, or stems scattered among other bryophytes, olive green to brown, glossy. **Stems** 180--250(--300) / μ m thick, branching lateral-terminal or less often ventral-intercalary; ventral surface (and sometimes dorsal) often with colorless rhizoids. **Leaves** inserted strongly obliquely (postical) and transversely (antical), not or weakly imbricate, strongly spreading, moderately secund, broadly ovate to suborbicular, weakly conduplicate, 0.75--0.83(--0.93) x 0.73--0.9(--0.98) mm, as wide or wider than long; lobes ovate-deltoid, about equal, sinus V-shaped, ca. 1/3--1/2 leaf length; central laminal cells 16--21(--25) x 13--16(--18) / μ m to ca. (10--11--13(--16) / μ m wide (marginal). smooth or cuticle verruculose, collenchymatous to strongly trigonous, basal cells more or less elongated, most longitudinally medial globose, elliptic or somewhat stellate; oil bodies (2--3--6(--8) per cell, broadly elliptic to orbicular, finely granular. **Underleaves** absent. **Specialized asexual reproduction** gemmae often present on margins of distal leaves, red to dark red, 1--2 celled, mostly angular, ca. 13--18 x 20--27 / μ m. **Sexual condition** dioicous. **Androecia** becoming intercalary, bracts imbricate, similar to vegetative leaves except often with a marginal tooth or appendage. **Gynoecia** becoming intercalary or terminal on leafy branches, bracts similar to the vegetative leaves but larger and sometimes 3-lobed, spreading from and not at all sheathing the perianth; perianths common, broadening upward and rounded at the apex, plicate only weakly near the mouth, mouth concolorous, lacerate with shortly ciliate lobes. **Sporophytes** occasional; capsule elliptic, wall of 3--4 cell layers, epidermal and interior wall cells with radial nodular thickenings, or innermost layer with semiannular thickenings. **Elaters** 2-spiral, ca. 8 / μ m wide. **Spores** finely papillose, 10--13 / μ m.

Rock walls, sandy soil, boulders by stream, old logs, decorticated log in *Thuja* swamp; 100--1800 m; Alta., B.C., N.B., Nfld. and Labrador (Labrador), N.S., Ont., Que.; Alaska, Conn., Ky,

Mass., Maine, Mich., Minn., N.H., N.Y., N.C., Tenn., Vt., Va., Wash., Wisc., W.Va., Wyo.; Eurasia.

6. *Anastrophyllum minutum* (Schreber) R. M. Schuster, Amer. Midl. Naturalist 42: 576. 1949
Jungermannia minuta Schreber, Fortsetz. Hist. Gronland, 285. 1770; *Sphenolobus minutus*
(Schreber) Berggren

Plants 1--3 cm long, (0.4--0.6--1(--1.5) mm wide (narrower flagellate stems often present). forming carpets or mounds, or (more often) stems scattered among other bryophytes, olive-brown, stramineous, orangish or reddish brown, not or slightly glossy, . **Stems** 125--175 / μ m thick, seldom branching (branches often arising from beneath gynoecia); rhizoids scarce and usually only on oldest portions of stems. **Leaves** transversely inserted, imbricate or not, spreading to recurved or incurved, more or less secund, elliptic, oblong-elliptic, depressed ovate-elliptic or suborbicular, canaliculate- or concave-conduplicate, 0.4--0.7 x 0.35--0.65 mm, longer than wide to wider than long; lobes ovate-deltoid to broadly ovate-deltoid, about equal, sinus V-shaped or U-shaped, ca. 1/4--1/3 leaf length; central laminal cells 18--26 x 15--20 / μ m to ca. 12--18(--20) / μ m wide (marginal), smooth, not or moderately collenchymatous, basal cells quadrate to short rectangular, medial quadrate to shortly rectangular; oil bodies 2--5(--6) per cell, elliptic to orbicular, granular. **Underleaves** absent. **Specialized asexual reproduction** lacking, though dispersing through fragmentation. **Sexual condition** dioicous. **Androecia** becoming intercalary, bracts imbricate, similar to vegetative leaves except more concave. **Gynoecia** becoming intercalary or sometimes remaining terminal, bracts 2--5 lobed 1/4--1/2 to base, lobes acute to acuminate and often dentate along margins, loosely sheathing the base of the perianth; perianths uncommon, cylindrical to cylindric-clavate, plicate near the mouth, mouth concolorous, shallowly lobed, lobes dentate. **Sporophytes** rare; capsule elliptic, wall of 3 cell layers, epidermal layer with xxx thickenings, the inner layers not observed. **Elaters** 2-spiral, to 8 / μ m wide. **Spores** lightly verrucose, (11--12--15 / μ m).

Essentially circumpolar. Greenland; Alta., B.C., Man., N.B., Nfld. and Labrador (Nfld.), N.S., N.W.T., Nun., Ont., Que., Yukon, Alaska, Conn., Idaho, Maine, Minn., NH, N.Y., N.C., Oreg., S.C., Tenn. Va., Vt., Wash., W.Va., Wyo.; Mexico; Eurasia; Atlantic Islands (Iceland).

The small leaf cells and 2-lobed leaves of the regularly branching shoots help characterize *Anastrophyllum minutum*. *Lophozia sudetica* is similar but *A. minutum* is distinguished by concentric rows of cells radiating from the lobe apices.

1. Leaves imbricate, 1.2--1.4 wider than long, split 0.4--0.5 the length, not folded; gemmae usually absent; lobe marginal cells 16--20 / μ m . . . 6a. *Anastrophyllum minutum* var. *minutum*
1. Leaves distant to touching, 0.8--1.2 wider than long, split 0.3--0.4 length, often folded; gemmae common; lobe marginal cells 12--16 / μ m . . . 6b. *Anastrophyllum minutum* var. *weberi*

6a. *Anastrophyllum minutum* (Schreber) R. M. Schuster var. **minutum**
Anastrophyllum minutum var. *grandis* (Gottsche ex Lindenber) R. M. Schuster

Leaves imbricate, hemispheric, 1.2--1.4 wider than long, split 0.4--0.5 the length, not folded, lobe marginal cells 16--20 / μ m. **Specialized asexual reproduction** usually absent, rarely by gemmae

Open or shaded sites, usually on siliceous rock in cold microclimates, hummocks in peatland, dry cliff crevice, heathland slope, stump; 0--1200 m; Greenland; Alta., B.C., N.B., Nfld. and Labrador (Nfld.), N.W.T., Ont., Que., Yukon, Alaska, Conn., Maine, Minn., N.Y., N.C., Tenn. Vt.; n Eurasia; Atlantic Islands (Iceland).

6b. *Anastrophyllum minutum* var. *weberi* (Martius) Karttunen, Ann. Bot. Fenn. 29: 119. 1992
Jungermannia weberi Martius, Fl. Crypt. Ilerlang., 157. 1817; *Sphenolobus nimutus* var. *weberi* (Martius) Schiffner

Leaves distant to touching, conduplicate-channeled, 0.8--1.2 wider than long, split 0.3--0.4 length, easily folded, lobe marginal cells 12--16 / μ m. **Specialized asexual reproduction** common, by gemmae.

Wet, shady rock walls; low to high elevations; Greenland; N.W.T., Alaska, Minn., N.C., Oreg., Tenn.; Mexico; n Eurasia; Atlantic Islands (Iceland).

7. *Anastrophyllum saxicola* (Schrader) R. M. Schuster, Amer. Midl. Naturalist 45: 71. 1951
Jungermannia saxicola Schrader, Syst. Samm. Cryptog. Gew. 2: 4. 1797; *Sphenolobus saxicola* (Schrader) Stephani

Plants 2--5 cm long, 1.2--2.5(--3) mm wide, forming carpets, or stems scattered among other bryophytes, olive green to orangish brown, glossy. **Stems** 240--380 / μ m thick, seldom branching (branches usually arising from beneath gynoecia); rhizoids scarce. **Leaves** inserted obliquely (postical) and transversely (antical); weakly to strongly imbricate, moderately spreading, weakly secund, depressed-ovate, concavely conduplicate, 0.5--0.8 x 0.77--1.2 mm, wider than long; lobes ovate-deltoid, about equal, sinus V-shaped, ca. 1/3--1/2 leaf length; central laminal cells 18--24 x (15--18--22 / μ m to ca. 17--20 / μ m wide (marginal), smooth, weakly to moderately collenchymatous, basal cells more or less elongated, medial shortly rounded-quadrate to hexagonal; oil bodies 2--4(--5) per cell, broadly elliptic to orbicular, finely granular.

Underleaves absent. **Specialized asexual reproduction** lacking, or plants dispersing through fragmentation. **Sexual condition** dioicous. **Androecia** becoming intercalary, bracts imbricate, similar to vegetative leaves except basally more or less saccate. **Gynoecia** becoming intercalary or terminal on leafy branches, bracts 2--5 lobed 1/4--1/3 to base, lobes acute to acuminate and dentate along margins, sheathing the base of the perianth; perianths rare, cylindrical to cylindrical-ovate, plicate near the mouth, mouth concolorous, lacerate with shortly ciliate lobes.

Sporophytes rare; capsule elliptic, wall of 3 cell layers, epidermal layer with nodulose thickenings, the inner layers with semiannular thickenings. **Elaters** 2-spiral, 8 / μ m wide. **Spores** lightly verrucose, 12--14 / μ m.

Acid rock, boulders, boulder slopes, hummocks, humus, cold shaded cliffs; 300--1500 m; Greenland; B.C., Nfld. and Labrador (Labrador); N.W.T., Yukon; Alaska, Maine, Minn., N.C., N.Y., Tenn.; Eurasia.

Anastrophyllum saxicola is similar to *Barbilophozia kunzeana* (Hübener) Müll. Frib., but the former is distinguishable by its lack of underleaves.

8. *Anastrophyllum sphenoloboides* R. M. Schuster, Hepat. Anthocerotae N. Amer. 2: 741. 1969

Schizophylloopsis sphenoloboides (R. M. Schuster) Váňa & L. Söderström

Plants 1--2 cm long, (0.5--0.7--0.95 mm wide, forming carpets or mounds, or stems scattered among other bryophytes, dark red-brown or reddish olive-brown. **Stems** (120--175--225 / μ m thick, unbranched or occasionally with a terminal *Frullania*-type branch; ventral surface with usually dense colorless rhizoids. **Leaves** transversely inserted, not or only weakly imbricate, basal portion sheathing, distal portion spreading, slightly secund, broadly elliptic-ovate to suborbicular, concavely conduplicate, 0.43--0.61 x 0.4--0.58 mm, as wide as long or slightly longer; lobes usually longer than wide, ovate-deltoid, about equal, sinus V-shaped, ca. 1/3--1/2 leaf length; central laminal cells 18--24(--26) x 14--19(--22) / μ m to ca. 15--19 x 13 / μ m wide (marginal), smooth or cuticle verruculose, collenchymatous to strongly trigonous, basal cells more or less elongated, most longitudinally rectangular, somewhat sinuose, medial rectangular to somewhat stellate; oil bodies 2--5(--6) per cell, spherical to elliptical, finely granular.

Underleaves absent. **Specialized asexual reproduction** absent. **Sexual condition** parocious and autoicous. **Androecia** becoming intercalary, bracts imbricate, similar to vegetative leaves except usually broader than long. **Gynoecia** terminal or sometimes becoming intercalary, bracts similar to the vegetative leaves but often broader than long and sometimes 3-lobed, loosely sheathing the base of the perianth; perianths common, broadest near middle and somewhat tapered to the mouth, plicate only near mouth; mouth not protruding, shortly lobed with denticulate margins.

Sporophytes common; capsule elliptic, wall of 3 cell layers, epidermal wall cells with strongly protruding nodular thickenings, or innermost layer with complete semiannular thickenings.

Elaters weakly 2-spiral, 6.5--9(--10) / μ m wide. **Spores** 12--15 / μ m.

Hummocks in rich fens, tundra; low to moderate elevations; Greenland; BC, Nfld. and Labrador (Labrador); N.W.T., Nun.; Alaska, Oreg.; n Eurasia.

Anastrophyllum sphenoloboides is characterized by reddish brown color, laminal cells with bulging trigones, and leaf base with elongate cells.

9. *Anastrophyllum tenue* H. R. Williams, Bryologist 71: 34. 1968 E

Crossocalyx tenuis (H. R. Williams) Schliakov, Novosti Sist. Nirsh. Rast. 15: 246. 1978

Plants 0.4--0.8 cm long, 0.4--0.55 mm wide (gemmiferous branches narrower), forming short mats or scattered among other bryophytes, light clear green, not or slightly glossy. **Stems** 120--155 / μ m thick, branching usually terminal and furcate (branches divergent and about equal thickness); ventral surface with abundant colorless rhizoids and mycorrhizal wefts. **Leaves** transversely inserted, not or weakly imbricate, strongly spreading, not or moderately secund, oblong-elliptic, suborbicular or depressed-elliptic, concave or almost flat, 0.3--0.33 x 0.3--0.36(--0.42) mm, wider than or as wide as long; lobes ovate-deltoid, about equal, sinus V- or U-shaped,

ca. 1/5--1/3 leaf length; central laminal cells 14--20 x (12--14--16 /um to l ca. 14--18 /um wide (marginal), smooth or faintly striolate, not or very weakly collenchymatous, basal cells shortly rounded-rectangular, medial shortly rounded-rectangular; oil bodies 5--7 or more per cell, elliptic to orbicular, faintly botryoid. **Underleaves** absent. **Specialized asexual reproduction** gemmae always present on slender, erect or ascending stems, dark red, 1--2 celled, cubic to pyramidal or irregularly angular, 12--20 /um. **Sexual condition** dioicous. **Androecia** becoming intercalary, bracts imbricate, orbicular or nearly so, sinus reaching 1/4--1/3 to base, toothed on one margin. **Gynoecia** rare, bracts 2-lobed, lobes entire; perianths pyriform, sulcate dorsally, mouth concolorous. **Sporophyte** not observed.

Calcicole; moderate elevations; Ont. (endemic)

10. SPHENOLOBOPSIS R.M. Schuster and N.Kitagawa, Nova Hedwigia 22: 152. 1972. [Greek *sphén*, wedge, and *lobós*, lobe, and *ópsis*, resemblance; alluding to cuneiform leaf lobes shared with *Sphenolobus*]

Steven L. Jessup

Plants minute, filiform; shoots 0.1--0.3(--0.45) mm wide, 0.5--1.5 cm long; isolated shoots or loose patches interwoven in mats with other cryptogams, or loosely to densely woven in pure mats; drab-green, yellow-green, green-brown, red-brown, dark-purple, or blackened, the shoot apices often verdant; prostrate, procumbent, ascending. **Stems** irregularly and remotely furcate; stem diameter (35--50--75 \um, cortical cells 15 x (12--16--24 \um, cortical cell walls evenly thickened; cuticle smooth to striate. **Branches** predominantly lateral-terminal, the branch replacing ventral lobe of lateral leaf, intermittently lateral-intercalary, the branch axillary and subtended by ventral lobe of lateral leaf, rarely ventral-intercalary; flagelliform shoots absent. **Leaves** transversely inserted, distichous, patent to erect, distant to loosely imbricate at shoot apices; leaf length 250--350 \um; leaf width 225--300 \um; bifid, lobes equal to subequal, conduplicate to spreading, cuneiform, acute, 4--7 cells wide, lobe apex comprising two superposed cells; sinus acute, triangular, sinus depth 0.5--0.8 leaf length; leaf margin entire, sporadically with a single tooth; leaf base decurrency absent; leaf cells subquadrate, 8--16(--20) x 12--20(--24) \um; trigones absent, cell walls evenly thickened; cuticle smooth to minutely roughened; oil bodies 2--6 per cell, minutely segmented, spherical to ovoid, diameter 2--4(6--8) \um. **Underleaves** reduced, obscure, absent on most stems, vestigial development appearing at stem base and below apex; filamentous, uniseriate, 1--2 celled, bearing 1--2 ephemeral apical papillae, lamina gradually enlarged in merophytes subtending gynoecia, becoming subequal with bracteoles. **Rhizoids** sparse or absent, scattered or in small loose patches proximal to underleaves, elongate, colorless. **Specialized asexual reproduction** absent. **Sexual condition** dioicous; populations often sterile, rarely androecial; gynoecial populations known from few localities; sporophytes very rare. **Androecia** developed as short terminal spikes on leading shoots, becoming intercalary; bract pairs 2--6; bracts larger than leaves, imbricate, ventricose; antheridium 1 per fertile bract; antheridium stalk uniseriate. **Gynoecia** on leading shoots; bracts gradually larger than leaves; bracteoles free, unlobed, lanceolate. **Perianth** tube cylindrical to rounded-trigonous at base, clavate, plicate distally; perianth mouth contracted, margin lobed, denticulate. **Perigynium** absent. **Seta** diameter 50 \um; outer cell rows 7-8; inner cells 1 or 2. **Capsules** yellow-brown, subglobose, ovoid to ellipsoidal; wall 2-stratose; wall cells bearing

yellow-brown nodular thickening on longitudinal and transverse radial walls. **Spores** 13--15 μm ; red-brown; minutely tuberculate. **Elaters** tapered to blunt; elater width 6--8 μm ; spiral bands 2.

Species 1: North America, Eurasia, Africa, Atlantic Islands.

Sterile non-gemmiparous strains of *Cephaloziella divaricata* having uniformly smooth cuticle and frequent lateral-terminal branches are distinct from *Sphenolobopsis* in having ventral leaves reduced to ligulae and develop throughout length of non-gemmiparous shoots, whereas ventral leaves in *Sphenolobopsis* are reduced to short filamentous appendages developed at shoot base and mature stem apices. Ventral leaves are absent or reduced to cellular papillae in non-gemmiparous shoots of *Anastrophyllum*. Presence of gemmae is diagnostic for *Anastrophyllum* (gemmae angular, 1--4 cells) or *Cephaloziella* (gemmae smooth, 2 cells). *Anastrophyllum* and *Cephaloziella* infrequently develop lateral-terminal branches whereas lateral-terminal branches predominate in *Sphenolobopsis*. Cuticular tubercles, papillae, verrucae, are frequent in strains of *Cephaloziella* and absent in *Sphenolobopsis*, with cuticle smooth, striate, or subtly verruculose. *Eremonotus myriocarpus* and diminutive *Marsupella spp.*, also non-gemmiparous, are distinct from *Sphenolobopsis* in absence of vestigial underleaves and frequent development of geotropic microphyllous shoots.

SELECTED REFERENCES Damsholt, K. 2002. *Sphenolobopsis*. In: Illustrated Flora of Nordic Liverworts and Hornworts. Nord. Bryol. Soc. Lund., pp. 156--158. Paton, J. A. 1999. *Sphenolobopsis*. In: The Liverwort Flora of the British Isles. Harley Books, Colchester, England. Schuster, R. M. 1980. *Sphenolobopsis*. In: Hepaticae and Anthocerotae of North America East of the Hundredth Meridian. New York. Vol. IV, pp. 7--17. Schuster, R. M., 2002. *Sphenolobopsis*. In: Austral Hepaticae Part II. Beih. Nova Hedwigia 119, pp. 340--343. Vána, J. and S. Piippo. 1989. *Sphenolobopsis*. In: Bryophyte Flora of the Huon Peninsula, Papua New Guinea. XXXI. Ann. Bot. Fennici 26: 287--288.

1. ***Sphenolobopsis pearsonii*** (Spruce) R.M. Schuster, Nova Hedwigia 22:152. 1972

Jungermannia pearsonii Spruce, J. Bot. 19: 33, 1881; *Cephalozia pearsonii* (Spruce) Stephani; *Cephaloziella pearsonii* (Spruce) Douin; *Cephaloziopsis pearsonii* (Spruce) Schiffner; *Sphenolobus pearsonii* (Spruce) Stephani

Plants in thin mats; dry plants wiry. **Leaves** and bracts sporadically bearing a tooth at base on antical or postical margin; leaf lobe apical cells often forming a 2-celled apiculus, 30--50 μm long, apical cell acute, 15--30 μm long.

Saxicolous and corticolous, sparsely to densely integrated in cryptogam mats with other liverworts, mosses and lichens, in cool-moist circum-acidic shaded habitats, adjacent to cool flowing water, cold air drainages, on humid shaded boulders and rock faces, on boles and understory branches in old growth forests of fog-drenched upper slopes and mountaintops; 0--2030 m: B.C. (Haida Gwaii, Pitt Isl.), Alaska (Aleutian Arch., Alexander Arch., Seward Pen.), N.C, Tenn., Va., Europe (England, Ireland, Norway, Scotland, Wales); Asia (Bhutan, Borneo,

Japan, Nepal, Russia in Siberia, Taiwan); Africa (Kenya, Malawi); Atlantic Islands (Faeroes, Tristan da Cunha); Pacific Islands (Papua New Guinea).

Among the smallest and rarest of liverworts, *Sphenolobopsis* is a globally dispersed hyperoceanic and montane waif known from widely scattered populations in archipelagoes and disjunct populations in insular cold-wet mountain environments. In North America known only from the highest peaks in Southern Appalachian Mountains, associated with *Abies fraseri* forests, and from a few widely scattered remote insular hyperoceanic populations in British Columbia and Alaska. Populations of *Sphenolobopsis* are usually sterile and do not develop gemmae. The plants apparently propagate and disperse by vegetative fragmentation. Neither gynoeical gametophytes nor sporophytes of *Sphenolobopsis* are known from North America.

11. TRITOMARIA Loeske, Hedwigia 49: 13. 1909

Won Shic Hong†

Pseudotritomaria Konstant. & Vilnet, *Saccobasis* H. Buch

Plants ca. 0.5--5 cm x 1--4 mm, prostrate to ascending. **Stem** transverse section with 1--3 cortical cells and 15--25 medullary cells; rhizoids numerous in dense mats, colorless to pale brown. **Leaves** subtransversely-obliquely inserted, 2--4-lobed, asymmetrical (except *T. polita*); lobes triangular, unequal, margins entire; cell walls collenchymatous, trigones bulging; oil bodies 3--8 per cell, finely granular, spherical to ovoid; underleaves absent. **Sexual condition** dioicous. **Specialized asexual reproduction** by gemmae. **Androecia** intercalary, antheridial stalk 1--2-seriate, female bracts leaflike, 3--4-lobed, margins entire-dentate, bracteoles usually absent. **Perianth** cylindrical-ovoid, plicate, mouth entire or ciliate. **Capsule** oval, walls 3--5-stratose, exterior wall with nodular and interior wall with semiannular bands. **Elaters** ca. 6--10 /um diam. **Spores** ca. 10--16 /um.

Species 8 (6 in the flora): North America, Europe, Asia, Africa.

The genus *Tritomaria* has been divided up by some authors; L. Soderstrom et al. (2016) treated these six species in four genera. In addition, R. E. Stotler and B. Crandall-Stotler (2017) have transferred two species of *Schistochilopsis* (*S. capitata* and *S. laxa*) into *Tritomaria*. The relevant alternate names are given in synonymy.

SELECTED REFERENCES

Schuster, R. M. 1969. *Tritomaria* Schiffn. In: R. M. Schuster. 1966--1993. The Hepaticae and Anthocerotae of North America. New York. Vol. 2, pp. 638--704. Schuster, R. M. 1984. Evolution, Phylogeny and Classification of the Hepaticae. In: R. M. Schuster, ed. 1984. New Manual of Bryology. Vol. 2, pp. 892--1070. Nichinan. Söderström, L., A. Hagborg, M. von Konrat et al. 2016. World checklist of hornworts and liverworts. *Phytokeys* 59: 1--828.

1. Leaves more or less symmetrical, equally 2--4-lobed with blunt to rounded apices; perianth mouth entire or subentire 5. *Tritomaria polita*

1. Leaves asymmetrical, unequally 2--3-lobed with acute or acuminate apices; perianth mouth dentate.

2. Leaves complicate to explanate, wider than long; gemmae rare-absent, yellowish-reddish brown.

3. Plants 1--1.5 mm wide, pellucid; leaves approaching symmetrical form, loosely complex, trigones coarsely nodose; gemmae angulate; perianth mouth teeth 1--2 cells long 4. *Tritomaria heterophylla*

3. Plants 2--3.5 mm wide, opaque; leaves asymmetrical, explanate, trigones moderate-bulging, but never nodose; gemmae generally absent; perianth mouth teeth 4--5 cells long 6. *Tritomaria quinquedentata*

2. Leaves canaliculate-complanate, longer than wide; gemmae abundant, reddish brown to rust red.

4. Leaves usually 3-lobed, lobes acute to subacute; trigones large; cilia of perianth mouth 1--4 cells long; gemmae reddish-brown
.. 3. *Tritomaria scitula*

4. Leaves asymmetrically 2--3-lobed, lobes acute or acuminate; trigones small; cilia of perianth mouth 5--6 cells long; gemmae rust-red.

5. Gemmae smooth, ovoid-elliptical; leaf cells 8--14 x 10--20 /um in midleaf; cell walls thick, trigones not bulging 1. *Tritomaria exsecta*

5. Gemmae angulate, polygonal; leaf cells 18--22 x 20--35 /um in midleaf; cell walls thin, trigones bulging 2. *Tritomaria exsectiformis*

1. *Tritomaria exsecta* (Schrader) Loeske, Hedwigia 49: 13. 1909

Jungermannia exsecta Schrader, Syst. Samml. Cryptogamischer Gewasche 2: 5. 1797

Plants ca. 0.5-- 2 cm x 1--2 mm, ascending, pale green to brownish green. **Stems** 0.2--0.3 mm diam., sparsely branching, transverse section with 2--3 cortical cells and 12--18 medullary cells; rhizoids numerous, colorless-pale brownish. **Leaves** succubous, distant to imbricate, conduplicate-concave, ovate to oblong-ovate, 0.8--1.2 x 0.5--0.8 mm, unequally 2--3-lobed

(median lobes often absent); antical lobes subulate, more weakly arched than postical lobe, sinus between middle lobes deeper (to 0.3 of the leaf length), margins entire, apex acuminate to acute; postical lobes ovate, more strongly arched than antical lobes, sinus between middle lobes very shallow (less than 0.1 of the leaf length), margins entire, apex acuminate to acute; cells rounded-rectangular, marginal cells 8--12 x 10--15 / μ m, median cells 8--14 x 10--20 / μ m, basal cells 10--15 x 15--30 / μ m, cuticle verruculose, walls thick, trigones small; oil bodies filling the lumen, 2--8 per cell, spherical to ovoid, 2--4 x 4--5 / μ m, finely granular, grayish; underleaves absent.

Specialized asexual reproduction by gemmae in masses at apices of shoots, rust-red, elliptical, 15--22 x 8--12 / μ m, 2-celled, smooth. **Sexual condition** dioicous. **Androecia** terminal, often with gemmae at tips, male bracts 4--10 pairs, similar to leaves, with antheridia, 1--2 androus, antheridial stalk 1-seriate. **Gynoecia** terminal, female bracts in few pairs, rounded-quadrate to broadly ovate, 3--5 lobed, equal or slightly smaller than leaves. **Perianth** cylindrical-obovate, 4--6-plicate, mouth ciliated with teeth 2--6 cells long. **Seta** 5 mm, capsule ovoid, walls 3-stratose, exterior walls with nodular thickenings, interior walls with annular thickenings, reddish brown. **Elaters** ca. 8 / μ m in diam., 2-spiral, reddish brown. **Spores** 9--12 / μ m, papillose, dark brownish.

Humic soil, humus on rocks, trunks and branches, especially *Alnus* and *Malus* in the West; 0--2000 m; Alta., B.C., N.B., Nfld., N.W.T., N.S., Ont., Que.; Alaska, Colo., Conn., Ga., Idaho, Iowa, Ky., Maine, Mass., Mich., Minn., Mont., N.H., N.Y., N.C., Ohio, S.C., Vt., Va., Wash., W.Va.; Mexico; e Africa.

In the East, *T. exsecta* is frequently associated with *Anastrophyllum minutum*, *A. michauxii*, *Bazzania trilobata*, *Diplophyllum apiculatum*, *Frullania asagrayana*, *Harpalejeunea ovata*, *Herbertus aduncus*, *Jamesoniella autumnalis*, *Lejeunea cavifolia*, *L. ulicina*, *Metzgeria crassipilis*, *Radula obconica*, *R. tenax*, and *Scapania nemorosa*. In the West it is associated with *Blepharostoma trichophyllum*, *Douinia ovata*, *Frullania nisquallensis*, *Scapania bolanderi*, and *S. umbrosa*.

2. *Tritomaria exsectiformis* (Breidler) Schiffn. ex Loeske, Hedwigia 49: 13. 1909

Jungermannia exsectiformis Breidler, Mitt. Naturwiss. Vereines Steiermark 30: 321. 1894

Plants ca. 0.5--3 cm x 1.5--2 mm, ascending, green to brownish. **Stems** 0.2--0.3 mm diam., sparsely branching, transverse section with 2--3 cortical cells and 12--18 medullary cells; rhizoids colorless to brownish. **Leaves** succubous, contiguous to imbricate, conduplicate-concave, ovate to oblong-ovate, 0.8--1.2 x 0.5--0.8 mm, unequally 2--3-lobed (median lobes often absent); antical lobes smaller than postical lobes, apex acuminate to acute, margins entire; cells rounded-rectangular, marginal cells 14--18 x 18--22 / μ m, median cells 14--22 x 20--35 / μ m, basal cells 20--25 x 28--40 / μ m, cuticle strongly verruculose, walls thin, trigones strongly bulging; oil bodies 5--12 per cell, spherical to ovoid, 3--5 x 4--6 / μ m, granular, grayish; underleaves absent. **Specialized asexual reproduction** by gemmae in masses at apices of shoots, rust-red or bright red, polygonal to pyriform, 12--25 x 10--25 / μ m, 2-celled. **Sexual condition** dioicous. **Androecia** terminal, often with gemmae at tips, male bracts similar to leaves, 3-lobed, with antheridia, 1--2 androus, antheridial stalk 1-seriate. **Gynoecia** terminal, female bracts larger than leaves, ovate, 3--4-lobed. **Perianth** free from the bracts, cylindrical, 4--6 plicate, mouth constricted, lobulate with teeth 2--5 cells long. **Capsule** ovoid, walls 2--4-stratose, exterior walls

with nodular thickenings, interior walls with semiannular thickenings, reddish-brown. **Elaters** ca. 7--10 / μ m diam., 2-spiral, reddish-brown. **Spores** 9--12 / μ m, papillose.

Subspecies 2 (2 in the flora): widely distributed across the northern part of the floral range.

1. Leaf cells 18--22 x 20--35 / μ m in midleaf; gemmae irregularly polygonal to pyriform, rust-red, 15--25 x 12--20 / μ m; widespread . . . 2a. *Tritomaria exsectiformis* subsp. *exsectiformis*

1. Leaf cells 14--16 x 20--25 / μ m in midleaf; gemmae angulate, bright reddish, 12--25 x 10--25 / μ m; arctic . . . 2b. *Tritomaria exsectiformis* subsp. *arctica*

2a. *Tritomaria exsectiformis* (Breidler) Loeske subsp. *exsectiformis*

Leaf cells 18--22 x 20--35 / μ m in midleaf; gemmae irregularly polygonal to pyriform, rust-red, 15--25 x 12--20 / μ m.

Creek banks, decayed wood, and humus over decayed wood in forests; 0--2300 m; Greenland; Alta., B.C., Nfld., N.W.T., N.S., Nun., Ont., Que., Yukon; Alaska, Colo., Conn., Idaho, Iowa, Maine, Mass., Mich., Minn., Mont., N.H., N.Y., N.C., Pa., Vt., Wash., Wis., Wyo.; Europe; Asia.

In the East, *Tritomaria exsectiformis* is frequently associated with *Bazzania trilobata*, *Lophozia ascendens*, *L. longidens*, and *Tritomaria exsecta*. In the West it is associated with *Blepharostoma trichophyllum*, *Cephalozia lunulifolia*, *Gymnomitrium coralloides*, *Lepidozia reptans*, *Lophozia incisa*, *L. ventricosa*, and *Ptilidium pulcherrimum*.

2b. *Tritomaria exsectiformis* subsp. *arctica* R. M. Schuster, Hep. Anthoc. N. Amer. 2: 661. 1969 E

Leaf cells 14--16 x 20--25 / μ m in midleaf; gemmae angulate, bright reddish, 12--25 x 10--25 / μ m. **Androecia, gynoecia and sporophyte** unknown.

Peaty soil with acidic rocks; 50--80 m; endemic to w Greenland.

The subsp. *arctica* is a North American endemic associated with *Anastrophyllum minutum*, *A. sphenoloboides*, *Cephalozia bicuspidata*, *Cephalozia divaricata*, *Lophozia opacifolia*, *Scapania lingulata*, and *Tritomaria quinqueidentata*.

3. *Tritomaria scitula* (T. Taylor) E. H. Jørgensen, Bergens Mus.Aarbok, Naturv. 7: 9. 1921

Jungermannia scitula T. Taylor, London J. Bot. 5: 274. 1846

Plants ca. 0.5--1.5 cm x 1.5--2 mm, prostrate-ascending, green-brownish. **Stems** 0.33--0.35 mm in diam., sparsely branching, transverse section with 1--2 cortical cells and 12--16 medullary cells; rhizoids numerous, colorless. **Leaves** succubous, imbricate, canaliculate, ovate-oblong, 0.7--1 x 0.6--0.8 mm, unequally 3-lobed (occasionally 2--4-lobed); lobes acute to subacute, sinus between lobes shallow (0.2--0.3 of the leaf length), apex rounded to truncated, margins entire;

cells subquadrate, marginal cells 16--22 x 24--30 / μ m, median cells 22--28 x 26--36 / μ m, basal cells 25--30 x 35--55 / μ m, cuticle verruculose, walls thin, trigones large (weakly bulging); oil bodies 4--10 per cell, spherical to ovoid, 5--8 x 5--10 / μ m, papillose; underleaves absent.

Specialized asexual reproduction by gemmae in masses at apices of shoots and tips of leaf lobes, reddish-brown, polygonal, 16--24 x 20--30 x 15--25 / μ m, 1--2-celled, smooth. **Sexual condition** dioicous. **Androecia** terminal, male bracts similar to leaves, 2-androus, antheridial stalk 1-seriate. **Gynoecia** terminal, female bracts larger than leaves, broadly oblong, 3--4-lobed with acute sinuses. **Perianths** cylindrical, 4--5-plicate, mouth ciliated with teeth 2--5 cells long. **Capsule** ovoid, wall 4-stratose, both outer and interior walls with nodular thickenings, yellowish-brown. **Elaters** ca. 9 / μ m in diam., 2-spiral, brownish. **Spores** 14--16 / μ m, papillose, brownish.

With other bryophytes on calcareous soil and decayed wood; 0--3500 m; e, w, nw Greenland; Alta., B.C., N.B., N.W.T., Nun., Que., Yukon; Alaska, Mich., Minn., Mont., Wis.; Europe.

The sporophyte of *Tritomaria scitula* is very rare. *Tritomaria scitula* is frequently associated with *Anastrophyllum minutum*, *Barbilophozia binsteadii*, *B. floerkei*, *B. lycopodioides*, *B. quadriloba*, *Blepharostoma trichophyllum* subsp. *brevirete*, *Cephalozia pleniceps*, *Jungermannia sphaerocarpa*, *Leiocolea heterocolpos*, *Odontoschisma macounii*, *Plagiochila asplenioides*, *Tritomaria exsectiformis*, *T. quinquidentata*, *Scapania cuspiduligera*, and *S. mucronata*.

4. *Tritomaria heterophylla* R.M. Schuster, Canad. J. Bot. 36: 272. 1958

Pseudotritomaria heterophylla (R. M. Schust.) Konstant. & Vilnet

Plants ca. 0.8--1.5 cm x 0.7--1.5 mm, ascending, brownish-purplish to brown. **Stems** 0.3--0.4 mm in diam., sparsely branching, transverse section with cortical and medullary cells; rhizoids numerous, colorless-pale brownish. **Leaves** succubous, imbricate, loosely complicate, transversely oblong, 0.7--0.9 x 0.8--1.2 mm, subequally 3-lobed, lobes ovate-triangular, sinus 0.2-0.3 of leaf length, apex acuminate to acute, margins entire or with scattered sharp teeth; cells rounded rectangular, marginal cells 20--25 / μ m, median cells 20--25 x 25--30 / μ m, basal cells 25--30 x 30--40 / μ m, cuticle weakly verruculose, strongly collenchymatous, trigones bulging; oil bodies 2--10 per cell, spherical to elliptical, 6--7 x 9--13 / μ m, finely papillose, grayish; underleaves absent. **Specialized asexual reproduction** by gemmae in masses at apices of juvenile leaves, reddish-brown, angular, 25--35 x 18--30 / μ m, 1--2 celled, smooth. **Sexual condition** dioicous. **Male bracts** similar to leaves, antheridia orange-yellow, antheridial stalk 1-seriate. **Gynoecia** terminal, female bracts larger than leaves, 2--5-lobed, lobes broadly ovate-triangular with entire margins. **Perianth** ovoid, plicate, mouth ciliated with teeth 2 cells long. **Sporophyte** unknown.

Peaty soil between rock clefts; 0--250 m; e, w, and n Greenland; Nun.

Tritomaria heterophylla is superficially similar to *T. scitula* and *T. quinquidentata*, and is frequently associated with *Aneura pinguis*, *Antheria juratzkana*, *Arnellia fennica*, *Blepharostoma trichophyllum* subsp. *brevirete*, *Cephalozia bicuspidata*, *C. pleniceps*, *Cephalozia arctica*, *Cryptocolea imbricata*, *Gymnomitrium concinatum*, *Jungermannia sphaerocarpa*,

Odontoschisma macounii, *Plagiochila arctica*, *Prasanthus suecicus*, *Scapania gymnostomophila*, and *Tritomaria quinquedentata*.

5. *Tritomaria polita* (Nees) Jørgensen, Bergens Mus. Aarbok 7: 4. 1921

Jungermannia polita Nees, Naturg. Eur. Leberm. 2: 9. 1836; *Saccobasis polita* (Nees) Buch

Plants ca. 1--1.5 cm x 2--3 mm, ascending, yellowish-green to reddish-brown. **Stems** 0.2--0.5 mm in diam., sparsely branching with *Frullania*-type, *Radula*-type and lateral-intercalary; transverse section with 1--3 elongated cortical cells and 10--16 medullary cells; rhizoids moderately numerous, colorless. **Leaves** transversely inserted, symmetrical, variously wider or narrower than long, broadly quadrate, ca. 1.7--2 x 1.4--1.7 mm, 3 or 2--4-lobed, sinus very shallow (0.1--0.25 of the leaf length), apex obtuse to rounded, margins entire; cells rounded-polygonal, marginal cells 15--25 x 25--35 / μ m, median cells 25--30 x 45--50 / μ m, basal cells 35--45 x 70--100 / μ m, cuticle weakly verruculose, walls thin, trigones large; oil bodies 2--12 per cell, spherical to ellipsoidal, ca. 5--10 / μ m, granular, grayish; underleaves absent. **Specialized asexual reproduction** by gemmae in masses at tips of leaf-lobes, yellow-brown to purplish, smooth or angulate, elliptical, ca. 28 / μ m, 1--2-celled. **Sexual condition** dioicous. **Androecia** terminal, male bracts, several pairs, similar to leaves, 3-lobed, lobes undulate. **Seta** 1--2 cm, capsule ovoid, exterior walls with nodular thickenings, interior walls with semiannular thickenings. **Elaters** ca. 8 / μ m in diam., 2-spiral, reddish-brown. **Spores** ca. 15 / μ m, reddish-brown.

Subspecies 2 (2 in the flora): North America, Europe, Asia.

1. Leaves uniformly 3-lobed with angulate sinuses, longer than wide; oil bodies 2--7 per cell; gemmae brown to purplish, angulate; female bracts 3-lobed; widespread 4a. *Tritomaria polita* subsp. *polita*

1. Leaves 2--4-lobed with curved sinuses, wider than long; oil bodies 8--12 per cell; gemmae usually absent, if present yellow brown, smooth; female bracts 2--4-lobed; sub-Arctic and Arctic 4b. *Tritomaria polita* subsp. *polymorpha*

5a. *Tritomaria polita* (Nees) Jørgensen subsp. *polita*

Leaves uniformly 3-lobed with angulate sinuses, longer than wide; oil bodies 2--7 per cell; gemmae brown to purplish, angulate; female bracts 3-lobed.

Exposed boulders, stream banks, soil on cliffs in forests, and seepage slopes in the tundra.; 500--1100 m; Greenland; Alta., B.C., Nfld. (Labrador), Nun., Que.; Alaska, Colo., Mont., Wash.; Europe; Asia.

The subsp. *polita* is frequently associated with *Barbilophozia kunzeana*, *Blepharostoma trichophyllum*, *Calypogeia azurea*, *Cephalozia bicuspidata*, *Diplophyllum albicans*, *Harpanthus flotovianus*, *Jungermannia atrovirens*, *Leiocolea heterocolpos*, *Lophozia guttulata*, *L. incisa*, *Pleuroclada albescens*, and *Tritomaria exsectiformis*.

5b. Tritomaria polita subsp. **polymorpha** R. M. Schuster, Hep. Anthoc. N. Amer. 2: 700. 1969

Saccobasis polymorpha (R. M. Schust.) Schljakov

Leaves 2--4-lobed with curved sinuses, wider than long; oil bodies 8--12 per cell; gemmae usually absent, if present yellow brown, smooth; female bracts 2--4-lobed. Sporophyte unknown.

Banks of small streams; 0--50 m; Greenland.

The subsp *polymorpha* is a North American endemic reported only from Greenland (R. M. Schuster 1988). It is frequently associated with *Blepharostoma trichophyllum* subsp. *brevirete*, *Cephalozia pleniceps*, *Leiocolea heterocolpos*, *Lophozia gillmanii*, *Odontoschisma elongatum*, *Scapania brevicaulis*, and *Tritomaria quinquedentata*. R. Grolle and D. G. Long (2000) treated this taxon as *T. polita*.

6. Tritomaria quinquedentata (Hudson) H. Buch, Mem. Soc. Fauna Fl. Fenn. 8: 270. 1932

Jungermannia quinquedentata Hudson, Fl. Angl. ed. 1: 433. 1762; *Lophozia quinquedentata* (Hudson) Cogniaux, *Trilophozia quinquedentata* (Huds.) Bakalin

Plants ca. 1.5--6 cm x 2-4 mm, ascending, green to yellowish-brown. **Stems** 0.3-0.45 mm in diam., sparsely branching, transverse section with 2--3 cortical cells and 10--14 medullary cells; rhizoids numerous, colorless. **Leaves** succubous, imbricate, ovate-reniform, 0.8--1.4 x 1--1.6 mm, unequally 3-lobed, shallow sinus (0.1--0.2 of leaf length), lobes broadly ovate, apex acute to apiculate, margins entire; cells rounded polygonal, marginal cells ca. 12--18 x 20--23 / μ m, median cells ca. 18--24 x 21--28 / μ m, basal cells ca. 20--28 x 28--38 / μ m, cuticle verruculose, walls thin, trigones distinct; oil bodies 2--10 per cell, spherical to ovoid, 4--7 x 5--10 / μ m, finely granular, grayish; underleaves absent. **Specialized asexual reproduction** by gemmae, rare, at tips of leaf lobes, yellowish-brown, polygonal, ca. 15--20 / μ m, 1--2-celled, smooth. **Sexual condition** dioicous. **Androecia** terminal, male bracts 4--12 pairs, similar to leaves, 2--3-androus, antheridial stalk 2-seriate. **Gynoecia** terminal, female bracts larger than leaves, 3--5-lobed, lobes acute. **Perianths** cylindrical-obovoid, plicate, mouth ciliated with teeth 4--5 cells long. **Seta** 2 cm, capsule oblong-ovoid, walls 4--5-stratose, yellowish or reddish-brown, exterior walls with nodular thickenings, interior walls with semiannular thickenings. **Elaters** ca. 6--7 / μ m in diam., 2-spiral, reddish-brown. **Spores** 12--15 / μ m, verruculose, yellowish-brown.

Varieties 3 (3 in the flora): North America, Eurasia.

1. Cells smaller, 18--24 x 21--28 / μ m in midleaf, trigones distinct; oil bodies 2--10 per cell; widespread . . . 6a. *Tritomaria quinquedentata* var. *quinquedentata*

1. Cells larger, 24--32 x 30--42 / μ m in midleaf, trigones bulging; oil bodies 7--20 per cell; sub-Arctic and Arctic.

2. Cells 25--30 x 30--42 / μ m midleaf; oil bodies 10--20 per cell . . . 6b.
Tritomaria quinquedentata var. *grandiretis*

2. Cells 24--26 x 32--45 / μ m in midleaf; oil bodies 5--15 per cell 6c.
Tritomaria quinquedentata var. *turgida*

6a. *Tritomaria quinquedentata* (Hudson) H. Buch var. **quinquedentata**

Plants green to yellowish-brown or pale brown. **Leaf cells** 18--24 x 21--28 / μ m in midleaf, trigones distinct but never bulging, oil bodies 2--10 per cell.

Wet humus over boulders, shaded cliffs, soil over exposed rock surface, decaying branches at the fringes of spray zones, and among heather on slopes; 0--1240 m; e, nw and sw Greenland; Alta., B.C., Man., N.B., Nfld. (Labrador), N.W.T., N.S., Nun., Ont., Que., Sask., Yukon; Alaska, Colo., Conn., Maine, Mich., Minn., Mont., N.H., N.Y., Oreg., Vt., Wash., Wis.; Europe; Asia.

The subsp. *quinquedentata* is frequently associated with *Anastrophyllum minutum*, *Barbilophozia attenuata*, *B. barbata*, *Tetralophozia setiformis*, *Diplophyllum taxifolium*, *Geocalyx graveolens*, *Gymnomitrium coralloides*, *Leiocolpos heterocolpos*, *Lophozia sudetica*, *Mylia taylori*, *Odontoschisma macounii*, *Plagiochila asplenioides*, *Ptilidium ciliare*, *Scapania americana*, *S. mucronata*, and *S. nemorosa*.

6b. *Tritomaria quinquedentata* var. **grandiretis** H. Buch & S. W. Arnell, *Svensk Bot. Tidskr.* 44 (1): 84. 1950

Plants pale and subpellucid. **Leaf cells** 25--32 x 30--42 / μ m in midleaf, trigones distinct, oil bodies 10--20 per median cell.

Acidic sites over peaty grounds near small stream; 0--500 m; nw and w Greenland.

The var. *grandiretis* is restricted to Greenland (R. M. Schuster 1958, 1988; R. M. Schuster and K. Dansholt 1974), where it is frequently associated with *Anastrophyllum minutum*, *Barbilophozia binsteadii*, *B. hatcheri*, *B. kunzeana*, *B. quadriloba*, *Lophozia ventricosa*, *Tritomaria quinquedentata* subsp. *quinquedentata*, and *Ptilidium ciliare*.

6c. *Tritomaria quinquedentata* var. **turgida** (Lindberg) Weimark, *Svensk Bot. Tidskr.* 31(3): 375. 1937

Jungermannia quinquedentata var. *turgida* Lindberg, *Köngl. Svenska Vetensk. Acad. Haandl.*, n.s. 23(5): 59. 1889; *Tritomaria quinquedentata* subsp. *turgida* (Lindberg) Damsholt

Plants uniformly strongly brownish. **Leaf cells** 24--26 x 30--45 / μ m in midleaf, trigones coarse and bulging; oil bodies 5--15 per cell.

Arctic and sub-Arctic fens, bogs, and on hillsides; 0--3400 m; e and nw Greenland; Yukon; Alaska; Asia (Siberia).

The var. *turgida* is frequently associated with *Antheria juratzkana*, *Barbilophozia binsteadii*, *B. kunzeana*, *Blepharostoma trichophyllum* subsp. *brevirete*, *Cephaloziella arctica*, *Lophozia*

ventricosa, and *Odontoschisma macounii*; The plants grow to 4 mm in width and the perianth is strongly ciliate-dentate with teeth 4--6 cells long, and 2--4-stratose at base in contrast to 1--3-stratose in subsp. *quinquedentata*.

12. DOUINIA (Jensen) H. Buch. Comment. Biol. 3(1): 13. 1928 * [For Charles Isidore Douin, French bryologist, 1858--1944]

Paul L. Redfearn, Jr. †

Plants small, olive green to yellow-green, leafy shoots 1.5--1.8 mm wide, dry plants curling up and away slightly from the substrate. **Stems** to 2 cm, cortex not clearly differentiated from interior region, cortical cells in 1--2 layers. **Leaves** alternate, +/- transversely inserted, complicately 2-lobed, fold not keeled and mostly not sheathing the stem, nearly, straight, ca 1/3 the length of ventral lobe; dorsal lobe, long narrow, triangular, sharply acute, usually entire; ventral lobe ovate, long, narrow, triangular, usually entire, much wider than dorsal lobe, usually 1.3--(1.1--1.7) times as long as dorsal lobe, sharply acute, usually entire; medial laminal cells of ventral lobe isodiametric, +/- 20 μ , walls not or little thickened, trigones small to medium. **Underleaves** absent. **Sexual condition** dioicous. **Sporophyte** capsule ovoid, 3--4-stratose. Elaters 1-spiral or only with rings, occasionally with 2 spirals that are not wound parallel with each other. **Spores** with blunt spines.

Species 1: North America, Europe, Asia.

Douinia is similar to *Diplophyllum*, but is distinguished by sharply acute leaf apices and a distinctive olive to yellow-green color and rather waxy appearance, perianth shape and mouth, leaf fold, apparent lack of gemmae, and its epiphytic ecology.

SELECTED REFERENCES Frye, T. C. and L. Clark. 1946. Hepaticae of North America. 6: 587--590. Seattle, Washington. Damsholt, K. 2002. Illustrated flora of Nordic liverworts and Hornworts. Lund, Sweden. Patton, J. A. 1999. Liverwort Flora of the British Isles. Martins, Great Horkelesley, Colchester, U.K. Potemkin, A. D. 1999. Circumscription of the family Scapaniaceae, with segregation of the new family Diplophyllaceae (Hepaticae). Ann. Bot. Fenn. 36: 271--283.

1. **Douinia ovata** (Dickson) H. Buch. Comment. Biol. 3(1): 14. 1928

Jungermannia ovata Dickson, Pl. Crypt. Brit. 3:11. 1793

Plants growing in patches or singly among other bryophytes. **Stems** 0.6--2 cm, prostrate to ascending, simple to +/- dichotomously branched, sometimes with innovations beneath the female perianths; cortical cells incrassate, the cuticular wall the thickest, interior cells thin walled; rhizoids few, present to near the stem tip, long, colorless. **Leaves** approximate to imbricate, fold straight to moderately concave, 250--460 μ , the angle rounded to obtuse; dorsal lobe transversely inserted, not decurrent, diverging 10--65° from the stem, moderately

appressed to stem, lanceolate with free tip narrowly triangular, 600--900 x 170--300 μ , curving to about middle of stem, apex sharply acute, margin usually entire, sometimes slightly crenulate to denticulate; ventral lobe margin slightly to distinctly lying over the lobe immediately behind it, little to moderately arched upward toward the stem, ending distinctly to usually strongly above the level of the base of the fold, not decurrent to barely decurrent, diverging 40--70° with the stem, ovate to narrowly ovate, 0.6--1 x 0.3--0.5 mm, 2--3.4 times as long as the fold, apex sharply acute, margin entire to occasionally crenulate with a few indistinct teeth; cells of middle and ventral half of leaf isodiametric, +/- 20 μ , distal cells 14--20 μ , 11--16 μ along ventral half, cavity rounded due to distinct trigones; oil bodies 3--8, covering 1/4--1/2 of the cell cavity; cuticle smooth to minutely verruculose, often giving the leaves a waxy appearance.

Sexual condition: male plants intermingled with female plants, more delicate, inflorescence usually terminal, bracts about 12, similar to leaves; female bracts with two equal lobes, somewhat larger than leaves of sterile shoots; perianth 3/4--5/6 emergent, ovoid to cylindrical-ovoid, deeply plicate to middle or below, with many lobes or long irregular branches that are often ciliate and antleroid, ultimate branches to 10 cells long. **Sporophyte** with capsule reddish brown to vinaceous red. **Spores** 12--21 μ .

Coastal regions, subarctic to Arctic in coniferous forest, shaded, siliceous rock outcrops of cliffs and trunks of conifers, hardwoods, among other mosses of high branches in suboceanic forests; 50--1350 m; B.C., Nfld. and Labr. (Nfld.); Alaska, Calif., Oreg., Wash.; Europe; Asia (Japan).

13. DIPLOPHYLLUM Dumortier, Syll. Jungerm. Eur. P. 44, 1871. Recueil d'Observations sur les Jungermanniacées 15. 1835 * [Latin *diplo* double, *phyllum* leaf, alluding to the folded leaf]

Jungermannia sect. *Diplophyllum* Dumortier, Syll. Jungerm. Eur. 44. 1831

Paul L. Redfearn, Jr†.

Plants usually in thin flat patches or mats. **Stems** with few intercalary and axillary branches, usually with subfloral innovations; cortex in 1--5 layers, cells somewhat to strongly flattened, smaller, more strongly thick-walled than medullary cells; branches few; rhizoids scattered, colorless. **Leaves** complicate-2-lobed with smaller dorsal and larger ventral lobes, not decurrent, the most proximal leaves usually smaller, rounded to apiculate, fold 1/4--1/2 the length of leaf, sheathing, nearly or almost parallel to the stem, distal half gradually curving outward 45--100° and becoming distinctly folded but not winged; ventral half of leaf narrowly lingulate, +/- falcate, 2--3.5:1; dorsal half similar but smaller and shorter; lobes strongly divergent, the dorsal 0--45° angle, narrowly obovate to lingulate; ventral lobes usually divergent at a 60--110°; leaf margins entire to more commonly finely crenulate to denticulate with small, sharp 1-celled teeth; cell walls little thickened at corners, marginal cells in several rows strongly, equally thick-walled; medial cells with small or inconspicuous trigones with slightly thickened or non-thickened walls, usually with conspicuous papillae, appearing nearly opaque compared to marginal cells; cells of the sheathing base elongate, 3--5:1; oil bodies distinctly segmented, appearing papillose, often absent in marginal cells, 2--5 per intramarginal cell, 10--16 or more per elongated cell. **Underleaves** absent. **Specialized asexual reproduction** by 1--2-celled, stellate gemmae with strongly protuberant angles. **Sexual condition** dioicous, rarely autoicous

or paroicous. **Androecia** with bracts imbricate in 4--8 pairs, similar to leaves, antheridia 1--3 per bract. **Gynoecia** terminal, bracts imbricate, similar to leaves; perianth ovate to cylindrical, +/- plicate, terete to slightly flattened near apex, apex denticulate, sometimes lobed or laciniate. **Sporophyte** capsule exerted on a short seta, ovoid, 3--5-stratose. **Spores** 11--15 μm , surface with irregular network of fine vermiculate, partly anastomosing markings, elevated at intersections as +/- weak tubercles; elaters 2-spiraled.

Species 24 (6 in the flora); North America, South America, Europe, Asia, Africa, Australia (Tasmania).

Diplophyllum is recognized by conduplicate, non-decurrent leaves with a defined marginal border, ventral lobes rounded-ovate, larger than dorsal lobes, underleaves absent; perianth cylindrical and distally pluriplicate (furrowed in subgenus *Macrodipllophyllum*, which has been transferred to *Scapania*). *Diplophyllum plicatum* is placed in the genus *Scapania* by A. D. Potemkin (1999).

SELECTED REFERENCES: Potemkin, A. D. 1999. Circumscription of the family Scapaniaceae, with segregation of the new family Diplophyllaceae (Hepaticae). *Annales Botanici Fennici* 36: 271--283. Schuster, R. M. 1975. The Hepaticae and Anthocerotae of North America east of the Hundredth Meridian 3: 177--232.

1. Leaves with margins entire; shoots 3--5(--8) mm, dry leaves slightly to strongly dorsally secund and connivent; perianth barely dorsiventrally flattened, gradually narrowed to a pointed apex6. *Diplophyllum andrewsii*

1. Leaves with margins distinctly crenulate or denticulate with projecting 1-celled teeth; shoots 5--25 mm, dry leaves slightly dorsally secund; perianth, +/- strongly dorsiventrally compressed, little to strongly contracted to mouth.

2. Leaf lobes with a sharply defined vitta of extremely elongate (60--70 μm) linear cells; cuticle often smooth or virtually so; cortex 3--5-stratose1. *Diplophyllum albicans*

2. Leaf lobes without a distinctly defined vitta of strongly elongated cells; cuticle distinctly papillose; cortex in 1--2 layers.

3. Ventral leaf lobes distinctly apiculate . . . 3. *Diplophyllum apiculatum*

3. Ventral leaf lobes rounded at apex, usually broadly so.

4. Dioicous, often sterile and gemmiparous; medial and submedial cells (distal to keel) of lobes short-rectangular, ca. 1.5--2:1; cells of apex of ventral lobes 7--10.5 μm ; gemmae at maturity greenish, 1--2-celled;. . . .2. *Diplophyllum taxifolium*

4. Autocious or parocious, perianths nearly always present; medial and submedial cells of ventral (and usually dorsal lobes) lobes sublinear, 2--4:1; cells of apex of ventral lobes 8--12 μm ; gemmae brownish at maturity (or absent).

5. Ventral lobes never truncate, not parallel-sided, distally broadly rounded; dorsal lobes often obtuse or subacute; medial leaf cells coarsely and closely papillose; perianth mouth with terminal cells not or barely elongate.. 4. *Diplophyllum obtusatum*

5. Ventral leaf lobes often truncate at apex, nearly or quite parallel-sided; medial leaf cells usually weakly papillose; perianth mouth with some terminal cells strongly elongate 5. *Diplophyllum obtusifolium*

1. *Diplophyllum albicans* (Linnaeus) Dumortier, Recueil d'Observations sur les Jungermanniacées, 16. 1835

Jungermannia albicans Linnaeus, Sp. Pl., 1133. 1753

Plants in compact to loose mats with crowded erect branches, 2--5 cm, green, golden yellow or deep brown, Arctic plants sometimes scorched, older portions frequently green, distal portions often reddish. **Stems** brownish, rigid, 1--5 cm, 0.2--0.3 mm in diameter, branches sparse, usually erect and simple; cortex 3--5 layers thick; leafy shoots 1.5--3.5 mm wide; rhizoids few. **Leaves** distinctly close together to imbricate, strongly complicate-2-lobed, strongly dorsally secund and connivent when dry, laterally spreading when moist, lobes with distinctly defined vitta of 4--6 rows of glistening, extremely elongated cells, 60--70 x 12--16 μm , leaf margins sparingly to strongly denticulate to serrate; marginal cells equally thick-walled, 13--22 x 12--14 μm , medial cells less thick-walled, 13--22 x 12--16 μm ; cuticle smooth to almost imperceptibly verruculose; dorsal lobes oblong-ovate to lingulate, apex obtuse to subacute, 0.5--1.5 x 0.25--0.45 mm, ca. 0.5 size of ventral lobe, erect; ventral lobes similar to dorsal lobes, very narrowly lingulate to oblong-ovate, rounded, obtuse to subacute at apex, 1--2 x 0.35--0.45 mm, widely spreading, frequently falcate, free lobe at 75--100° angle with stem. **Specialized asexual reproduction** by abundant gemmae, usually restricted to excurrent apices of vittae, 1-celled, stellate, usually yellowish green, becoming fuscous in scorched Arctic plants. **Sexual condition** dioicous. **Androecia** short, bracts 4--8 pairs, often reddish, antheridia 1--2 per bract. **Gynoecia** bracts similar to leaves but somewhat larger; perianth half exerted at maturity, distally narrowed and plicate, mouth lobes lobulate, ending in cilia bearing 1 to several 1-celled teeth at base. **Sporophyte** capsule ovoid. **Spores** 11--15 μm , papillose, yellowish brown.

Shaded, humid logs, tree trunks, noncalcareous rock walls; 0--500 m. Greenland; B.C., N.B., Nfld. and Labr. (Nfld.), N.S., Nunavut, Yukon; Alaska, Oreg., Maine, Wash.; Europe; Asia; Atlantic Islands.

Diplophyllum albicans has an oceanic distribution in the coniferous biome north to the Arctic tundra.

2. *Diplophyllum taxifolium* (Wahlenberg) Dumortier, Recueil d'Observations sur les Jungermanniacées, 16. 1835

Jungermannia taxifolia Wahlenberg, Flora Lapponica, 389. 1812

Plants in thin, extensive patches, green to yellowish brown. **Stems** 1--3.5 cm, 0.16--0.3 mm in diameter, prostrate at base, ascending distally; slightly branched below perianth; cortex 1--2 layers thick; leafy shoots 1.3--2.4 mm wide; rhizoids few. **Leaves** equal in size, close together to subimbricate, lobes 0.33--0.5:1, dry leaves +/- dorsally secund; dorsal lobe appressed to stem, spreading laterally at an angle of 10--40 °, elliptic, 0.43--0.65 x 0.18--0.35 mm, male shoots 0.6--0.8 x 0.26--0.36 mm on female shoots, tapering distally to a bluntly obtuse or somewhat rounded apex, rarely acute, varying from nearly entire to denticulate, dorsal base closely and sharply crenulate-denticulate in distal fifth by projecting cells, ca. 1/2 as long as ventral lobe; ventral lobe horizontally spreading, nearly flat, somewhat falcate, distal half spreading at an angle of 65--110° on mature leaves, lingulate-elliptic, parallel-sided for about the medial third, somewhat tapering in the apical fifth to a broadly rounded, bluntly obtuse apex, often more pointed on male and gemmiparous plants, 0.75--0.9 x 0.28--0.36 mm on males shoots, female shoots 1--1.2 cm, 0.35--0.45 mm wide, margins with scattered denticulations on apical portion, sometimes nearly entire, basal half distinctly sharply crenulate by projecting cells; keel suberect, gradually spreading outward; marginal cells of ventral lobe 7--10 μm near apex, mostly isodiametric, equally thick-walled, forming a slightly to obscure pachydermous border; cells on middle ventral half ca. 1.5--2:1, 18--25 x 10--15 μm , occasionally longer, trigones none or minute; cuticle moderately papillose, papillae often extending onto marginal cells, 6--12 per cell in leaf middle; oil bodies absent in 1--2 marginal cell rows, 2--3 in the next rows to 3--8 in cells of leaf middle to 10--15 in elongated basal cells. **Specialized asexual reproduction** common, as masses of 2-celled gemmae at apex of shoots, on lobe margins of distalmost leaves, yellowish green, polygonal and stellate because of blunt projecting angles, gemmiparous leaves often twice the normal size. **Sexual condition** dioicous, largely sterile, male and female plants usually in separate patches, distinctly heterothallic, male plants smaller. **Androecia** with bracts in 5--6 or more pairs, similar to normal leaves, but ventral with lobe often more tapering and pointed, dorsal lobe covered with wart-like papillae, antheridia usually 2 per bract, 1 often aborted. **Gynoecia** terminal, bracts slightly larger than stem leaves; perianth 0.5--0.75 exerted at maturity, ovate, dorsiventrally compressed, plicate in distal half, a dorsal sulcus extending to near base, strongly contracted to mouth, lobed, dentate, hyaline, occasionally entire. **Sporophyte** capsule ovoid, brown. **Spores** 13--15 μm , closely coarsely verruculose, pale brown.

Varieties 3 (3 in the flora): widely distributed in the northern hemisphere.

1. Ventral lobes abruptly mucronate with a 1-celled mucro, or triangularly narrowed and then mucronate.2c. *Diplophyllum taxifolium* var. *mucronatum*

1. Ventral lobes broadly rounded.

2. Cuticle covered with many small cuticular papillae, leaves not very opaque.
 . . .2a. *Diplophyllum taxifolium* var. *taxifolium*

2. Cuticle medially on the leaf with coarse, dense papillae, leaves very opaque except on margins.2b. *Diplophyllum taxifolium* var. *macrosticta*

2a. *Diplophyllum taxifolium* var. *taxifolium*

Ventral lobes rounded; cuticle with small, numerous papillae; leaves not very opaque.

Shaded rocks, cliffs, soil banks, humus, often along streams; 0--1950 m; Greenland; B.C., N.B., Nfld. and Labr., N.S., Ont.; Alaska, Conn., Maine, Mass., Minn., N.H., N.Y., N.C., Tenn., Vt., Wash., W.Va.; Europe; Asia.

2b. *Diplophyllum taxifolium* var. *macrosticta* H. Buch, Commentat.Observ. Jungerm. 3(1): 23. 1928

Ventral lobes rounded, papillae dense, cells very opaque except marginally.

Moist, shaded rock walls and ledges, soil; 1860--2010 m; N.S.; Alaska, Maine, Minn., Tenn., Vt.; Europe; Asia.

2c. *Diplophyllum taxifolium* var. *mucronatum* R. M. Schuster, Hepaticae and Anthocerotae of North America, East of the Hundredth Meridian 3: 203, plate 334. 1974 **E**

Leaves abruptly mucronate with a 1-celled mucro, or triangularly narrowed and then mucronate, cells rather opaque.

Shaded rocks; 1645 m; N.C.

3. *Diplophyllum apiculatum* (A. Evans) Stephani, Spec. Hep. 4:110, 1910 **E**

Diplophylleia apiculatum A. Evans, Bot. Gaz. 34: 372, plate 12. 1902

Plants in patches, green in shade to brownish or reddish in sun. **Stems** 0.3--1 cm, 0.15--0.2 mm in diameter, prostrate, apices weakly ascending, sparingly branched; cortex poorly defined, 1--2 layers thick; leafy shoots 1.5--2.4 mm wide; rhizoids numerous below. **Leaves** nearly equal in size along the entire stem, imbricate to subimbricate; dorsal lobe diverging at an angle of 10--40°, appressed, elliptic, 0.23--0.48 x 0.13--0.23 mm, ca. 1/2 size of ventral lobe, apex triangularly narrowed and usually strongly apiculate, margins irregularly denticulate, rarely entire; ventral lobe horizontal, sometimes weakly dorsally secund when dry, +/- falcate and gradually spreading, apical half spreading 65--105°, narrow and lingulate-pointed, with nearly parallel sides, 0.5--0.75 x 0.2--0.3 mm, averaging 2.5:1, apex triangularly narrowed, usually strongly apiculate, terminated by a tooth often 2 cells long, margins +/- sparingly denticulate toward apex, distinctly crenulate along basal half of ventral margin; marginal cells of apex nearly

isodiametric, 12--16 x 9--14 μm , strongly thick-walled in 3--5 rows, inner cells gradually thin-walled, not collenchymatous, 16--23 x 12--14 μm ; cuticle smooth on margins, but slightly to distinctly minutely papillose in medial parts of lobes, papillae oval, mostly 6--12 per cell in central part of lobe; oil bodies of marginal and submarginal cells small, 3--6 per cell, 10--20 in medial, on submedial and +/- elongate cells, almost filling the lumen making the cells very opaque. **Specialized asexual reproduction** common, gemmae in dense clusters, on apical parts of lobes of distalmost leaves, 1--2-celled, polygonal with rounded protuberances, +/- stellate in outline, always green. **Sexual condition** autoicous. **Androecia** usually on main shoots, bracts 2--4 pairs, similar to leaves, strongly inflated proximally, antheridia 1 per bract. **Gynoecia** usually on short lateral intercalary branches, originating below male shoots, bracts similar but larger than normal leaves, 5 pairs, distal 2--3 pairs suddenly larger than lower pairs; perianth 1/2 or more exserted, obovoid, somewhat dorsally flattened, apical half 4--6-plicate, gradually narrowed toward an irregularly lobed mouth, lobes dentate-laciniate with teeth 1--3 cells long. **Sporophyte** capsule ovoid, red--brown. **Spores** 12--14 μm , minutely verruculose, yellow-brown.

Two varieties are recognized by R. M. Schuster (1974).

Varieties 3 (2 in the flora): temperate North America and eastern Asia.

1. Ventral leaf lobes +/- tapering, mostly acute to apiculate, usually gradually so, medial leaf cells with small to moderate-sized papillae, cell outlines clearly distinguished; marginal cells prominently thick-walled, forming a vague border; lowland form 3a. *Diplophyllum apiculatum* var. *apiculatum*

1. Ventral lobes rounded, +/- suddenly (rarely gradually) apiculate to mucronate medial leaf cells with 2--6 coarse, juxtaposed papillae, virtually hiding the cell outlines; marginal cells scarcely thick-walled, not forming a border; upland form 3b. *Diplophyllum apiculatum* var. *taxifolioides*

3a. *Diplophyllum apiculatum* var. *apiculatum* E

Ventral lobes +/- tapering, mostly acute to apiculate, papillae of leaf cells delicate, medial leaf cells prominently clearly distinguished, marginal leaf cells prominently thick-walled.

Moist shaded soil banks, acidic rocks, beneath ledges, shaded vertical exposures, rarely on rotting logs; 120--1400 m; Ont.; Ala., Ark., Conn., D.C., Ga., Ind., Kans., Ky., Maine, Md., Mass., Mich., Minn., Miss., Mo., N.J., N.Y., N.C., Ohio, Pa., R.I., S.C., Tenn., Vt., Va., W.Va., Wis.; Asia (Japan).

Diplophyllum apiculatum var. *apiculatum* is endemic to the deciduous forests of eastern North America.

3b. *Diplophyllum apiculatum* var. *taxifolioides* R. M. Schuster, *Hepaticae and Anthocerotae of North America, East of the Hundredth Meridian* 3: 214, plate 338, figs. 1, 3, 8--10, 12, plate 340, figs. 6--15. 1974 E

Ventral lobes rounded, usually suddenly apiculate, leaf cells with 2--5 coarse, juxtaposed papillae virtually hiding the cell outlines.

Shaded humus of damp ledges; 1860--1920 m; N. C., Tenn.

R. M. Schuster (1974) suggested the possibility that this variety is a hybrid between *D. apiculatum* and *D. taxifolium*.

4. *Diplophyllum obtusatum* (R. M. Schuster) R. M. Schuster, Hepaticae and Anthocerotae of North America, East of the Hundredth 3: 215. 1974

Diplophyllum apiculatum var. *obtusatum* R. M. Schuster, Amer. Midl. Nat. 49: 432. 1953

Plants in small, depressed mats or patches or creeping among other bryophytes, green in shade to purplish or reddish brown in sun, proximal leaf bases tending to become vinaceous even when plants otherwise green. **Stems** 0.5--1.2 cm, 0.16--0.26 mm in diameter; prostrate with ascending tips, branching on one or both sides, or from below or axils female bracts or from older portions of stems; cortex 2-stratose; leafy shoots 0.8--2 mm wide; rhizoids scattered, frequent, long. **Leaves** subimbricate, often closely so in androecial region, weakly to moderately secund when dry; ventral lobes lingulate, free distal half diverging 55--95° with stem, not parallel-sided and widest before apex, distally broadly rounded, often obtuse or subacute, 0.69--1.1 x 0.36--0.45 mm, 3--4 /x as long as fold; medial and submedial cells sublinear, 2--4:1, cells of apex 8--12 μ m, margins distinctly denticulate except above junction with keel, rarely subentire, proximal margins strongly denticulate with sharp, jagged, often curved 1-celled teeth; dorsal lobe obliquely or erect spreading, 15--55°, appressed, elliptic, obovate to short-lingulate, usually rounded at apex, occasionally apiculate to subacute, 0.42--0.46 x 0.22--0.26 mm, margins +/- finely denticulate, keel weakly arched; cells at apex and margins 10--12 μ m, medial and submedial cells sublinear, 2--4:1, 11--14 x 15--18 μ m, in proximal part of leaf forming a weakly defined "vein," opaque because of numerous large oil-bodies and chloroplasts; marginal and submarginal cells strongly and evenly thick-walled, inner cells often thinner walled with minute trigones; cuticle of medial coarsely and closely papillose; oil bodies absent in most marginal cells, 3--6 in medial cells. **Specialized asexual reproduction** by numerous, mostly 1-celled gemmae, spheric to ovoid, thick-walled, green becoming brownish at maturity, approximately stellate in outline. **Sexual condition** monoicous, usually autoicous, very rarely paroicous. **Androecia** bracts in 2--5 pairs, similar but smaller than stem leaves, more imbricate, strongly ventricose at base, antheridia 1--3 per bract. **Gynoecia** on terminal or separate branches, bracts in 2--5 pairs, similar but larger than stem leaves; perianth +/- flattened, ovoid to obovoid, short, contracted to mouth, 6--9 plicate, upper 1/3--1/4 narrowed, mouth denticulate with 1--rarely 2--celled rigid teeth. **Sporophyte** not seen.

Rock outcrops; moderate to high elevations; Nfld. and Labr. (Nfld.), Ont.; N.C., Minn., Tenn.; Central America (Costa Rica); Asia (Japan).

5. *Diplophyllum obtusifolium* (Hooker) Dumortier, Recueil d'Observations sur les Jungermanniacées, 16. 1835

Jungermannia obtusifolia Hooker, Brit. Jungerm., plate 26, 1816

Plants in patches or among other bryophytes, light green in shade to yellow, chestnut or red-brown in sun, in direct sunlight, locally vinaceous pigmented at ventral lobe bases. **Stems** 0.8--1 cm, branches abundant, prostrate; leafy shoots 1.5--2.5 mm wide; cortex 1--2 layers thick, rhizoids abundant on ventral surface of stem, abundant, often near ventral leaf bases. **Leaves** contiguous to imbricate, often dorsally secund, lingulate, often truncate at the apex, but occasionally +/- apiculate; ventral lobes 0.5--1.5 x 0.35--0.5 mm, ca. 2 x as large as dorsal lobes, lingulate, nearly or quite parallel-sided, often weakly falcate, diverging 75--90° from stem, proximal margins distinctly irregularly denticulate at proximal base, +/- finely denticulate at apex, apices rounded-truncate; dorsal lobes 0.3--0.9 x 0.4--0.7 mm, ca. 0.6 x the ventral lobe in area, diverging from the stem at +/- 30° and often directed almost to the stem apex, +/- appressed to stem and lobe, lingulate to ovate-lingulate, margins finely denticulate, at least near apex; cells firm, rather opaque, ca. 10 μm at leaf tip, marginal cells 8--12 μm , medial and submedial cells sublinear, 2--4:1, ca. 40--64 x 12--16 μm ; cuticle usually +/- papillose; oil bodies spheric to ovoid, 2--5 per medial cell. **Specialized asexual reproduction** usually absent or very rarely by stellate, 1-celled gemmae. **Sexual condition** parocous. **Androecia** bracts in 3--5 pairs, similar to stem leaves, lingulate lobes, antheridia 1--3 per bract. **Gynoecia** bracts in 3--5 pairs, similar stem leaves; perianth plicate, short-clavate to oblong clavate, contracted to mouth, shallowly 5--6-lobulate, shallow lobes bearing 1--3, mostly 1-celled teeth; **Sporophyte** capsule ovoid. **Spores** 8--12 μm , delicately papillose-verrucose.

Moist shaded soil banks and boulders; 15--600 m; Greenland; B.C.; Alaska, Calif., Oreg., Wash.; Europe; Asia (Japan).

Diplophyllum obtusifolium is distributed across temperate and subarctic regions.

6. *Diplophyllum andrewsii* A. Evans, Bryologist 25: 28, plate 1, figs. 1--11, 1922

Plants in small patches, +/- shining pale to yellow-green, translucent in shade, becoming clear, translucent, often golden brown in sun. **Stems** prostrate with apices ascending, 0.5--2.5 cm, 0.15--0.22 mm in diameter, irregularly and sparingly branched below perianth, cortex 1--2 layers thick; leafy shoots 1.3--2.4 mm wide; rhizoids dense on prostrate stems. **Leaves** with entire margins, loosely to closely imbricate in the shade, when moist, nearly flat and spreading horizontally, strongly dorsally secund and connivent in the sun, the opposed ventral lobes with their tips often closely overlapping; dorsal lobes when moist suberect to obliquely spreading 10--45° angle with the stem, when dry oblong--ovate to short-lingulate, squarrose, broadly rounded at apex, 0.65--0.8 x 0.4--0.45 mm, up to 0.5 x as large as ventral lobe; ventral lobes widely spreading, at a 80--110° angle with the stem, oblong-lingulate, 1--2 x 0.5--0.6 mm, 2:1, +/- strongly concave, margins raised at least in sun forms, keel short suberect, nearly straight to slightly curving outward near apex; marginal cells in several rows, isodiametric, thick-walled, ca. 10 μm ; medial cells thin-walled with indistinct concave-sided trigones, 20--23 x 14--16 μm ; cuticle almost smooth, papillae of medial cells very pale, minute and inconspicuous; oil bodies, homogenous, glistening, spheric to short-ovoid in distal fourth of lobes and submarginal cells, 4--6 per cell, 6--10 in medial and submedial cells. **Specialized asexual reproduction** by

fragmented branches, gemmae very rare, small, spheric to subspheric, +/- brownish. **Sexual condition** autoicous, abundantly fertile. **Androecia** bracts in 4--6 pairs, similar to stem leaves, antheridia 1 per bract. **Gynoecia** on short lateral branches, bracts in 2--5 pairs of increasingly larger leaves, similar to but somewhat larger than stem leaves; perianth at maturity 1/2 exerted, oblong to fusiform, irregularly 8--10-plicate, barely dorsiventrally flattened, gradually contracted to somewhat pointed, mouth irregularly and shallowly 10 or more lobed, lobes acuminate, ending in cilia formed by 2--5 elongated cells, sides of lobes with 1--2-celled sharp teeth. **Sporophyte** unknown in North America.

Shaded loamy soil of eroding banks along streams, rock ledges and crevices; 270--1700 m; N.C., S.C., Tenn., Va.; Japan.

14. MACRODIPLOPHYLLUM (Buch) Persson, Svensk Bot. Tidskr. 43: 507. 1949 [Latin *macro*, large, Latin *diplophyllum*, doubled leaf, alluding to a related genus with conduplicate leaves]

David H. Wagner

Plants 10--110 x 2--4 mm, ascending to erect, in tufts or scattered among other bryophytes, yellowish green to pale olive green or greenish brown, sometimes tinged red near apex. **Stems** 300--400 x 350--500 μm ; outer cortical cells thick walled in (1--)2--4 layers, yellowish green near apex, becoming dark brown to black with age, branches few, lateral or ventral, often as paired innovations below gynoecia. **Leaves** contiguous to imbricate, complicate 2-lobed with smaller dorsal and larger ventral lobes, dorsal to ventral lobe length ratio 0.3--0.9; **dorsal lobe** 2 x 1 mm, subtransversely inserted, insertion line extending partially across stem to wrapping around opposite side of stem, decurrent to 0.2 width of stem or not decurrent, spreading 30--80° from stem axis, obliquely obovate, oblong to strap shaped, usually slightly convex, outer margin parallel to line of keel, 0.5--2 mm; **ventral lobe** to 2.8 x 1.6 mm, transversely inserted, insertion line slightly arched, not decurrent or decurrent to 0.1--0.2 of stem width, midline spreading 60--90° from stem axis, oblong, obliquely obovate to spatulate, straight or weakly falcate, slightly convex, spreading to deflexed; keel strong, not winged, straight to curved, 0.25--0.7 of ventral lobe length; margins entire to strongly but unevenly spinose-dentate, apices often eroded from gemma production; cells at leaf base elongate rectangular, trigones bulging with nodose cell walls, to 95 x 25 μm ; median cells cells polygonal, mostly isodiametric, usually with bulging trigones, 30 x 25 μm , marginal cells with evenly thickened walls usually forming a distinct border in 2--3(--4) rows, one species without a definite border; cuticle rarely nearly smooth, usually striolate to verruculose, in one species strongly papillose; oil bodies 2--10 per cell, usually finely granulate, rarely of amorphous texture, clear to pale brown. **Specialized asexual reproduction** by gemmae, produced in masses on leaf margins at shoot apex, 2--4 celled, angular, rounded polygonal or oval, outer walls thick, inner walls intersecting. **Sexual condition** dioicous; sporophytes rarely observed. **Androecia** terminal, rarely observed, unknown in most species, male bracts similar to vegetative leaves but gibbous, closely overlapping. **Gynoecia** terminal, often producing paired innovations below unfertilized perianth, female bracts in one

pair, similar to vegetative leaves but larger and more prominently dentate. **Perianth** rare in most species, cylindrical to slightly flattened, pluriplicate to the base or occasionally plicate only in distal half, weakly dorsiventrally compressed, mouth lobulate or lacerate with slender, sometimes branched, lobulae to 20 cells long. **Capsule** with walls 3--4(--5) stratose, elaters 2-spiral, spores 15--18 / μ m, minutely punctate or verruculose.

Species 5 (5 in the flora), close to Pacific Ocean in an arc from Japan and Korea north through Russian Far East, sporadically to Yakutia and Baikal Siberia, across the Aleutian Archipelago and down the west coast of North America to northern California.

The genus *Macrodiplophyllum* is distinguished by its robust habit, rounded, lingulate leaf lobes, elongated basal laminal cells, perianth pluriplicate usually to the base, perianth mouth constricted and lobulate or lacinate-ciliate, with few to many branched cilia. It is a member of cool temperate rain forest ecosystems, primarily terrestrial on peaty soil, in crevices between rocks, on cliff faces, and occasionally corticolous on tree bases or downed logs. It is a natural biogeographic group characterized by an array of ancestral traits. Molecular phylogenetic analysis shows that *Macrodiplophyllum* in a broad sense is derived from the more generalized genus *Diplophyllum* and is basal to two more specialized genera, *Douinia* and *Scapania* (Heinrichs et al. 2012). Alternate classifications would place the three historically recognized species of *Macrodiplophyllum* in *Diplophyllum* (Hong 1980), all in *Scapania* (Potemkin 2002), or assign one species to *Scapania* and two to *Douinia* (Konstantinova et al. 2013). The two recently described species, *M. flaccidum* and *M. rubrum* (Wagner 2016), have yet to be subjected to molecular phylogenetic analysis.

SELECTED REFERENCES Choi, S. S., V.A. Bakalin, and B. Sun. 2012. *Scapania* and *Macrodiplophyllum* in the Russian Far East. *Bot. Pacifica* 1: 31--95. Heinrichs, J., A. Bombosch, K. Feldberg, H. P. Kreier, J. Hentschel, J. Eckstein, D. Long, R.L. Zhu, A. Schäfer-Verwimp, A. R. Schmidt, B. Shaw, A. J. Shaw and J. Váňa. 2012. A phylogeny of the northern temperate leafy liverwort genus *Scapania* (Scapaniaceae, Jungermanniales). *Mol. Phylog. Evol.* 62: 973--985. Konstantinova N. A., A. A. Vilnet, L. Söderström, A. Hagborg, M. J. von Konrat. 2013. Notes on Early Land Plants Today. 14. Transfer of two *Macrodiplophyllum* species to *Douinia* (Scapaniaceae, Marchantiophyta). *Phytotaxa* 76(3): 31--32. Potemkin, A. D. 2002. Phylogenetic system and classification of the family Scapaniaceae Mig. emend. Potemkin (Hepaticae). *Ann. Bot. Fenn.* 39: 309--334. Vilnet, A. A., N. A. Konstantinova and A. V. Troitsky. 2011 ["2010"]. Molecular insight on phylogeny and systematics of the Lophoziaceae, Scapaniaceae, Gymnomitriaceae and Jungermanniaceae. *Arctoa* 19: 31--50. Wagner, D. H. 2016. Two new species of *Macrodiplophyllum* (Marchantiophyta) endemic to western North America. *Phytoneuron* 2016-57: 1--22.

1. Dorsal lobe base reaching across stem, the base tightly wrapped around stem opposite the keel; ventral lobe base with a well-defined strip of thick-walled marginal cells armed with closely set, slender, unicellular, spinose teeth; spinose strip often strongly red pigmented.

2. Cuticle faintly striolate to verruculose; leaves contiguous, evenly spaced so the keel is usually exposed at stem to leaf junction; midline of distal half of ventral lobes spreading

55--85° from stem; spinose strip at base of ventral lobe usually bright orange-red5.

Macrodiplrophyllum rubrum

2. Cuticle strongly papillose with several globose papillae over each median cell; leaves mostly imbricate with few keels exposed; midline of distal half of ventral lobes spreading 80--90° from stem; spinose strip at base of ventral lobes not pigmented 2.

Macrodiplrophyllum microdontum

1. Dorsal lobe base reaching 0.5--0.9 across stem but not wrapped around opposite side; ventral lobe base entire or with scattered marginal teeth, low or up to 4 cells in length, not spinose; margins not pigmented or at most light pink.

3. Dorsal lobes 0.8--0.9 as long as ventral lobes, about as broad as ventral lobes; margins uniformly entire 4. *Macrodiplrophyllum imbricatum*

3. Dorsal lobes less than 0.7 as long as ventral lobes, much narrower than ventral lobes; margins sparsely to moderately dentate, at least at apex of lobes.

4. Distal half of ventral lobe spreading less than 75° from stem; lobes with small, inconspicuous teeth; leaf form changed little upon drying3.

Macrodiplrophyllum plicatum

4. Distal half of ventral lobe spreading close to 90° from stem; both lobes regularly dentate, teeth usually prominent at lobe apices; leaves wilted and contorted when dry1. *Macrodiplrophyllum flaccidum*

1. *Macrodiplrophyllum flaccidum* D.H. Wagner, Phytoneuron 2016-57: 8. 2016 E

Plants 20--60 x 2--4 mm, ascending to erect, yellowish green to pale olive green, sometimes tinged red near apex. **Stems** 335--370 x 235--260 μm , outer cortical cells thick walled in 2--4 layers, olive green at apex, dark brown to black below, sparsely branched. **Leaves** contiguous to mostly imbricate; dorsal to ventral lobe length ratio 0.5--0.7; dorsal lobe 1.2--1.6 x 0.5--0.8 mm, subtransversely inserted, insertion line weakly arched, weakly decurrent for 0.1--0.2 of stem width, midline smoothly curved from base to apex, spreading 30--80° from stem axis, obliquely obovate to arcuate, flat to slightly convex, apex obtuse to rounded, basal margin reaching across stem not quite to opposite side; ventral lobe 1.4--1.9 x 0.4--0.9 mm, transversely inserted, insertion line slightly arched, decurrent for 0.1--0.2 of stem width, midline spreading 60--90° from stem axis, obliquely obovate to spatulate, weakly falcate, slightly convex, contorted when dry; keel curving evenly from base, often dark brown to black, 0.3--0.5 of ventral lobe; cells at leaf base elongate-rectangular, 36--40 x 18-20 μm , trigones strongly bulging, walls nodose; median cells (15--20--26(--27) μm , trigones bulging, margins with evenly thick walled cells in 2--3 cell rows, finely dentate with few teeth at lobe bases but teeth regularly produced on distal third except where eroded by gemma production, apex of ventral lobe with occasional multicellular teeth; cuticle smooth; oil bodies 2--3(--4) per cell, reniform-fusiform, amorphous texture, pale brown, nearly filling cell lumen. **Specialized asexual reproduction** not known. **Sexual condition** dioicous. **Androecia** occasional, becoming intercalary, male bracts average 6,

similar to vegetative leaves but strongly gibbous at base. **Gynoecia** terminal, female bracts like vegetative leaves but larger and more prominently dentate-spinose. **Perianth** frequent, deeply plicate in distal half only, long emergent, mouth lacerate with slender, sparsely branched lobulae up to 8 cells long.

Wet rocks or soil between rocks, often on streamside cliffs; 0--975 m; B.C.; Alaska, Wash.

Macrodiplphyllum flaccidum is most similar to *M. plicatum* in morphology and ecology. Both occur almost exclusively on inorganic substrates such as cliff faces, boulders, and sandy soil. One of the most distinctive characters of *M. flaccidum*, dry and contorted leaves, is seen only in dried specimens. Therefore, it is more easily recognizable in the herbarium than in the field. The presence of a prominent black keel and black stem is suggestive but not diagnostic. Whereas most species of this genus have at least some roughening of the cuticle, striolate, verruculose to papillose, the cuticle of *M. flaccidum* is usually quite smooth making the plants appear glossy or shiny when dry. Dry specimens of *M. plicatum* have a distinctly velvety or satiny appearance.

2. *Macrodiplphyllum microdontum* (Mitten) Persson, Svensk Bot. Tidskr. 43: 507. 1949

Martinellius microdontus Mitten, Trans. Linn. Soc. London, Bot. 3: 196. 1891; *Diplphyllum microdontum* (Mitten) H. Buch; *Scapania microdonta* (Mitten) Müller Freib.

Plants 30--70 x 4--4.4 mm, ascending to erect, yellowish green to brownish green or fuscous brown. **Stems** 300--350 x 500--550 μm , outer cortical cells thick walled in 2--4 layers, yellowish green near apex and fuscous brown below, sparsely branched. **Leaves** closely imbricate; dorsal to ventral lobe length ratio 0.5--0.6; dorsal lobe 1.6--2 x 0.8--1 mm, subtransversely inserted, insertion line slightly arched, weakly decurrent for 0.1--0.2 of stem width, spreading 35--50° from stem axis, obliquely oblong to ovate, slightly convex, apex rounded, basal margin auriculate, curving over stem and wrapped around opposite side; ventral lobe 2--2.6 x 1.2--1.6 mm, transversely inserted, insertion line slightly arched, decurrent for 0.1--0.2 of stem width, midline angled 70--85° from stem axis, obliquely oblong to obovate, slightly convex; keel 0.25--0.35 of ventral lobe, semicircularly arched, diverging 30--50° from stem axis at the base, curving away to 110--140° at the distal end; cells at leaf base elongate, 50--75 x 18--25 μm , trigones strongly bulging; median cells 25--37 x 25--30 μm , trigones strongly bulging, marginal cells with bulging trigones like median cells; ventral lobe base with a well defined marginal border of thick-walled cells 2--5 cells wide extending up to 1 mm from point of insertion, armed with closely set, slender, unicellular, sometimes recurved spinose teeth, denticulate to dentate at apex with sharp, unicellular teeth over 2 times longer than wide, sometimes eroded by gemma production; oil bodies 4--6(--8) per cell, spherical to elliptical, 5.5--7.5 x 5--6 μm , granulose. **Gemmae** uncommon, produced in masses at apices of leaves, oval to rounded polygonal, 2--4 celled, brown. **Sexual condition** presumed dioicous. **Androecia** not known. **Gynoecia** terminal. **Perianths** rare, deeply plicate, long emergent, mouth lobulate-ciliate, the lobululae 8--16 cells long.

Arctic and subarctic; shaded rocks, cliffs, crevices in gravelly barrens; 0--1500 m; B.C., Yukon; Alaska; Asia (Russian Far East, Southern Siberia).

Macrodiplophyllum microdontum is distinctively characterized by dramatically large, bulbous papillae crowded on the cuticle of the leaves. This species is sparsely distributed over a wide area. Plants bearing perianths have not been seen in North America.

3. *Macrodiplophyllum plicatum* (Lindberg) Persson, Svensk Bot. Tidskr. 43: 507. 1949

Diplophyllum plicatum Lindberg, Contr. Fl. Crypt. As., 235. 1872; *Scapania plicata* (Lindberg) Potemkin; *Douinia plicata* (M. Howe) Konstantinova & Vilnet

Plants 20--60 x 2--4.8 mm, in small patches, ascending to erect, yellowish green to brownish green. **Stems** 300--350 x 500--550 μm , outer cortical cells thick walled in 2--4 layers, yellowish green near apex and fuscous brown below, sparsely branched, mostly ventral. Leaves contiguous to mostly imbricate; dorsal to ventral lobe length ratio 0.4--0.5; dorsal lobe 1.2--1.6 x 0.5--0.8 mm, subtransversely inserted, insertion line weakly arched, weakly decurrent for 0.1--0.2 of stem width, spreading 35--50° from stem axis, obliquely obovate, lingulate to spatulate, flat to slightly convex, apex rounded, basal margin reaching across stem to opposite side; ventral lobe 2.0--2.8 x 0.9--1.4 mm, transversely inserted, insertion line arched, not decurrent, midline spreading 70--85° from stem axis, obliquely obovate to spatulate, weakly falcate, slightly convex; keel 0.3--0.4 of ventral lobe length, diverging 10--30° from stem axis at base and gradually curving up to 80--100° at the end; cells at leaf base elongate, 30--70 x 17.5--35 μm , trigones bulging; median cells 18--32.5 x 17--25 μm , trigones bulging, evenly thick walled cells in 2--3 cell rows at margin, margins denticulate to dentate at least at apex of ventral lobe; cuticle striolate to verrucose; oil bodies 5--8(--10) per cell, spherical to elliptical, granulose. **Gemmae** uncommon, produced in masses at apices of leaves, distinctly angular, 2(--4) celled, brown. **Sexual condition** presumed dioicous. **Androecia** not known. **Gynoeceia** terminal, female bracts in one pair, larger than sterile leaves, dorsal lobe to 1.7 mm, ventral lobe to 2.9 mm. **Perianth** rare, cylindrical, pluriplicate, weakly dorsiventrally compressed, 4--5 x 1--12 mm, mouth shallowly lobulate, lobe margins dentate with 1--3 celled teeth.

Terrestrial, on shaded rocks, crevices in gravelly barrens, humus along stream bed or coniferous forest floor; 0--915 m; B.C.; Alaska, Wash.; Asia (Japan, Russian Far East).

Macrodiplophyllum plicatum is most similar to *M. flaccidum*. The dense, finely granular papillae on the cuticle of *M. plicatum* gives leaves when dry a satin like sheen, in contrast to the glossy dried leaves of *M. flaccidum*. The keel of *M. plicatum* is moderately curved while that of *M. flaccidum* curves in a semicircle. The dorsal and ventral lobes of *M. plicatum* are both relatively straight and diverge at differing angles from the stem while the lobes of *M. flaccidum* curve away in a parallel fashion. Habitat and substrate are quite variable over the range of the species. The typical form has lingulate leaves that are sparingly dentate. There is an uncommon form which has broader, more obovate and more strongly dentate lobes, occurring throughout the range of the typical form. It is more often found on tree bases than the typical form; it will likely prove to be distinct upon further study.

4. *Macrodiplophyllum imbricatum* (M.A. Howe) Persson, Svensk Bot. Tidskr. 43: 508. 1949

Scapania imbricata M. Howe, Bull. New York Bot. Gard. 2(6): 104. 1901; *Diplophyllum imbricatum* (M. Howe) Müller Freib. ex Stephani; *Douinia imbricata* (M. Howe) Konstantinova et Vilnet; *Diplophyllum hyalinum* Brinkman ex Frye et Clark

Plants 10--40 x 2.5--3.5 mm, in tufts, ascending to erect, olive green to brownish green. **Stems** 400--450 x 250--350 μm , outer cortical cells thick walled in 1--2(3) layers, olive green at apex, fuscous brown below, sparsely branched. **Leaves** closely imbricate; dorsal to ventral lobe length ratio 0.8--0.9; dorsal lobe 1.1--1.5 x 0.6--0.7 mm, subtransversely inserted, insertion line weakly arched, not decurrent, angled 30--50° from stem axis, obliquely obovate to spatulate, slightly convex, apex rounded, basal margin curving over stem to opposite side; ventral lobe 1.6--1.8 x 0.7--0.8 mm, transversely inserted, insertion line arched, not decurrent, midline angled 60--80° from stem axis, obliquely obovate to spatulate, slightly falcate and convex, apex rounded; keel 0.3--0.4 of ventral lobe length, diverging 10--30° from stem axis at base and gradually curving up to 90--110° at the end; cells at leaf base elongate-rectangular, 62.5--85 x 20--25 μm , trigones bulging to nodose; median cells 25--25 x 20--29 μm , trigones bulging, evenly thick walled cells in 2--3 cell rows at margin, margins entire throughout; cuticle striolate to weakly verrucose; oil bodies (3--4--5(--7)), mostly spherical, granulose. **Gemmae** rare, produced in masses at apices of leaves, spherical to angular, 2--4 celled, brown. **Sexual condition** presumed dioicous. **Androecia** not known. **Gynoecia** not known.

Montane to subalpine, on shaded rocks in stony fields, open rocky hillsides, or crevices in gravelly barrens; 0--1400 m; B.C.; Alaska; Asia (Russian Far East).

Macrodipllophyllum imbricatum has strictly entire leaf margins, unique in the genus. Also distinctive are the dorsal lobes being as broad or broader than the ventral lobes and consistently so closely inserted that the keel is never visible without dissection. Only the broad lobed form of *M. plicatum* is likely to be mistaken for this species; *M. plicatum* always has margins dentate at least at the apex of ventral lobes.

5. *Macrodipllophyllum rubrum* D. H. Wagner, Phytoneuron 2016-57: 1. 2016 E

Plants 20--110 x 2--4 mm, ascending to erect, in tufts or scattered among other bryophytes, yellowish green to pale olive green. **Stems** 440--520 x 320--350 μm ; a single layer of outer cortical cells thick walled, olive green at apex, dark brown to black below, branches lateral, frequently produced as paired innovations subtending unfertilized gynoecia. **Leaves** imbricate-sheathing at base, spreading, distally pectinate, not imbricate; dorsal to ventral lobe length ratio 0.45--0.7; keel nearly straight and parallel to antical margin of lobes, 0.45--0.7 of ventral lobe length; dorsal lobe 1.1--1.5 x 0.6--0.7 mm, subtransversely inserted, insertion line weakly arched, not decurrent, spreading 40--55° from stem axis, oblong to strap shaped, slightly convex, apex rounded, lobe base auriculate, reaching across stem and tightly wrapped around opposite side; ventral lobe 2.0--2.6 x 0.8--1.2 mm, transversely inserted, insertion strongly line arched, decurrent to half the stem width, midline angled 55--85° from stem axis, strap shaped, apex rounded, strongly convex, often deflexed when dry; cells at leaf base elongate-rectangular, 75--95 x 17--20 μm , trigones bulging, cell walls nodose thickened; median cells (18--20--23(--27)) μm , trigones concave to moderately bulging, margins evenly thick walled cells in 2--3 cell rows, more strongly thickened at base of ventral lobe, where 2--5 cells wide, extending up to 1 mm

from point of insertion, armed with closely set, slender, unicellular, sometimes recurved spinose teeth, the spinose strip usually strongly red pigmented at tip of shoot, darkening with age; cuticle striolate to weakly verrucose; oil bodies 5--8(--10) per cell, spherical to elliptical, granulose.

Gemmae frequent, produced in masses at apices of leaves, spherical to rounded polygonal, 2(--4)-celled, pale tan. **Sexual condition** dioicous. **Androecia** not known. **Gynoecia** terminal, female bracts in one pair, larger than sterile leaves, dorsal lobe to 1.7 mm, ventral lobe to 2.9 mm; small bractlets sometimes included. **Perianth** occasional, deeply plicate to base, long-emergent, mouth lobulate-ciliate, lobulae branched, slender, sharp tipped, 6--10(--20) cells long, 1--4 cells wide.

Restricted to organic substrates; most common on bark of trees near their base and on decaying logs in coniferous forests or in more northern sites on peaty humus; 0--700 m; B.C.; Alaska, Calif., Oreg., Wash.

The frequent occurrence of *Macrodiplophyllum rubrum* on tree bases is in striking contrast to the predominantly rock and soil substrates favored by all other species of the genus. The most prominent diagnostic characteristic of this species, the bright red, spinose margin of the ventral lobes, is quite easily detected in the field with a hand lens. Although superficially quite different in general appearance, *M. rubrum* shares some fundamentally distinctive characters with *M. microdontum*: strongly differentiated, broad, spinose margin at the base of the ventral lobe and a dorsal lobe that wraps around the stem. Their ranges do not overlap.

15. SCAPANIA (Dumortier) Dumortier, Recueil Observ. Jungerm. 14. 1835 * [Greek *scapanion*, spade, alluding to the shape of the perianth]

Alexey D. Potemkin

Stem with 1--5-stratose, slightly to sharply defined cortex with walls slightly thickened to bastfiber-like, cells pigmented or not pigmented, usually with smaller lumen and thicker walls than intracortical cells. **Leaves** entire to dentate and ciliate distally or basally, with distinctly acute to occasionally rounded keel; ventral lobe rounded to ovoid and lingulate, rarely lanceolate, subtransversely or arcuately inserted, non-decurrent, short to long-decurrent; median leaf cells thin- to occasionally thick-walled, with indistinct to coarsely bulging trigones, (8--15--25(--35) μ m wide; vittae never present; cuticle smooth to moderately and coarsely papillose. **Specialized asexual reproduction** by gemmae, 1--2(--4 or 8)-celled, ovoid to rarely angular, exceptionally spheric. **Sexual condition** dioicous (rarely monoicous). **Perianth** mostly compressed to occasionally inflated, contracted to truncate at mouth, eplicate to pluriplicate; mouth laciniate-ciliate to entire. **Androecia** on main shoot. **Capsule wall** 2--7-stratose. **Elaters** 2(--3)-spiral.

Species about 90--100 (37 in the flora): mainly Northern Hemisphere.

Identification of *Scapania* is made difficult by the plasticity of the species, rather exacting criteria for identification, and considerable dependence on plant maturity for manifestation of many characters (H. Buch 1928; R. M. Schuster 1974). It is thus important that identifications be

determined by a combination of many characters, of which some characters require special definitions. The shape of leaf lobes is given here by their width/length ratio. Lobe length corresponds to the length of the line segment from the lobe apex through the keel curvature to the stem; lobe width is a perpendicular to the line of lobe length in the broadest lobe sector. Length of a leaf lobe or gemma is measured from the point of connection with the plant, and is not simply the longest dimension. Often width of leaf lobes is greater than length. Lobe angle is the angle between the line defining the lobe length and the stem. Considerable variability of lobe angle persuades me to avoid exact measurements and use subjective definitions. When it is small (to ca. 25°), the lobe is considered to be subparallel to the stem. If it is mostly larger, the lobe is described as divergent with the stem. Dorsal and ventral lobes are described as subparallel to each other when their angles with the stem differ slightly. The keel is usually an angulate area of leaf fold between lobes. It forms a lower lobe margin, grading occasionally into a keel wing, i. e., a strip several cells broad proximal to the keel. The keel is measured from its insertion to its distal end. When the keel is strongly arched such a measurement may represent a sum of lengths of several line segments. Degree of its change from keel base to distal end predetermines keel curvature identification, i. e., keel indistinctly, moderately or strongly arched.

Oil body characters are very useful in identifying fresh material. Oil body persistence is also a convenient character for identification of herbarium materials. In some species oil bodies persist for a very long time, often for 50--100 years. In most species, however, oil bodies disintegrate in several months after collecting; oil bodies usually are preserved in the herbarium longer if the specimens were dried gradually in natural conditions without special devices such as a dryer and freezer. Moistening of dried specimens may lead to quick oil body disintegration.

The degree of plant maturity affects the size of the plants, leaf measurements and proportions. Juvenile plants usually have more narrow leaf lobes, and slightly arched and often relatively longer keels (because of shorter ventral lobe). In the Arctic some species may exist as immature or impoverished phenotypes. This often hampers their correct identification. In such cases, oil body characteristics and field observations are particularly important. For detailed descriptions of Arctic *Scapania* see R. M. Schuster (1974, 1988), and R. M. Schuster and K. Damsholt (1974).

The infrageneric classification and the order of infrageneric taxa accepted below follows mainly A. D. Potemkin (2002) except the genus *Macrodiplophyllum* (H. Buch) Persson, which is treated separately in this flora.

North American *Scapania* species fall into 13 sections. Species 1--3 are sect. *Nemorosae* (K. Müller (Freiburg)) Buch, species 4 sect. *Gracilidae* Buch, species 5--6 are sect. *Aequilobae* (K. Müller (Freib.)) Buch; species 7 belongs to sect. *Compactae* (K. Müller (Freiburg)) Buch; species 8--10 are sect. *Calcicolae* Schuster; species 11--12 are sect. *Planifoliae* (K. Müller (Freiburg)) Potemkin; species 13--15 are sect. *Ciliatae* Grolle; species 16--20 are sect. *Scapania*; species 21 and 22 belong to sect. *Cuspiduligerae* Buch and *Plicaticalyx* (K. Müller (Freiburg)) Potemkin respectively; species 23--30 are sect. *Curtae* (K. Müller (Freiburg)) Buch; species 34--36 are sect. *Scapaniella* (Buch) Potemkin; species 37 belongs to sect. *Incurvae* Potemkin. Because of within-group variability, a key to species is given rather than to sections. The species known for the flora only on the basis of doubtful records are marked by asterisks (*).

SELECTED REFERENCES Buch, H. 1928. Die Scapanien Nordeuropas und Sibiriens 2. Systematischer Teil. Soc. Sci. Fennica, Comm. Biol. 3(1): 1--177. Heinrichs, J., A. Bombosch, K. Feldberg, H.-P. Kreier, J. Hentschel, J. Eckstein, D. Long, R.-L. Zhu, A. Schäfer-Verwimp, A. R. Schmidt, B. Shaw, A. J. Shaw, & J. Váňa. 2012. A phylogeny of the northern temperate leafy liverwort genus *Scapania* (Scapaniaceae, Jungermanniales). *Molecular Phylogenetics and Evolution* 62: 973--985. Konstantinova, N. A, A. A, Vilnet, L. Söderström, A. Hagborg, M. J. von Konrat. 2013. Notes on Early Land Plants Today. 14. Transfer of two *Macrodiplophyllum* species to *Douinia* (Scapaniaceae, Marchantiophyta). *Phytotaxa* 76 (3): 31--32. Müller, K. 1905. Monographie der Lebermoosgattung *Scapania* Dum. *Nova Acta Acad. Caes. Leop.-Carol.* 83: 1--312. Müller, K. 1951--1958. Die Lebermoose Europas. Rabenhorst's Kryptogamen Flora, 3rd ed. 6. Potemkin, A. D. 1998. On the origin, evolution and classification of the genus *Scapania* (Dum.) Dum. (Hepaticae). *J. Hattori Bot. Lab.* 85: 243--271. Potemkin, A. D. 1999. An analysis of the practical taxonomy of some critical northern species of *Scapania* (Scapaniaceae, Hepaticae). *Bryologist*. 102(1): 32--38. Potemkin, A. D. 2002. Phylogenetic system and classification of the family *Scapaniaceae* Mig. emend. Potemkin (Hepaticae). *Ann. Bot. Fenn.* 39: 309--334. Schuster, R. M. 1974. The Hepaticae and Anthocerotae of North America east of the hundredth meridian. Vol. 3. Vilnet, A. A., N. A. Konstantinova, and A. V. Troitsky. 2010. Molecular insight on phylogeny and systematics of the Lophoziaceae, Scapaniaceae, Gymnomitriaceae and Jungermanniaceae. *Arctoa* 19: 31--50.

1. Keel rounded at least basally.
 2. Marginal sector of ventral leaf base hyaline, without chloroplasts and oil bodies. 21. *Scapania cuspiduligera*
 2. Marginal sector of ventral leaf base not hyaline, its cells having chloroplasts and oil bodies.
 3. Ventral lobe distinctly decurrent proximal to the keel insertion . . . 17. *Scapania obscura* (in part)
 3. Ventral lobe not decurrent proximal to keel insertion, subtransversely or arcuately inserted .
 4. Marginal cells of mature non-gemmiparous leaves thin-walled like median cells.
 5. Ventral lobes broader, (0.6--0.75--1.2 times as wide as long, rounded to blunt at apex.
 6. Often monoicous; trigones variable, acute to bulging; purple pigmentation absent; dorsal lobe mostly 0.9--1.2 times as wide as long and extending to far edge of stem and occasionally beyond (if dorsal lobe 0.55--0.9 times as wide as long, then not extending to far edge of stem) 7. *Scapania compacta* (in part)
 6. Dioicous; trigones acute; purple pigmentation of ventral leaf base common; dorsal lobe 0.6--0.95 times as wide as long, not extending to far edge of stem.
 7. Leaves entire or crenulate from gemma production, never denticulate; gemmae broadly ovoid, 12--24 x 14--36 μm , green to purple 28. *Scapania obcordata*
 7. Leaves more or less often denticulate distally; gemmae more or less narrowly ovoid, 11--20 x 18--38 μm , green, sometimes reddish in sun 27. *Scapania curta* (in part)

5. Ventral lobes narrower 0.4--0.75(--0.8) times as wide as long, more or less sharply apiculate.
8. Specialized asexual reproduction by gemmae uniformly 1-celled, smaller, 7--11 x 11--18 μm ; ventral lobe narrow, 0.45--0.6 times as wide as long; xylicolous36. *Scapania apiculata* (in part)
8. Specialized asexual reproduction by gemmae 2-celled, larger, 10--19 x 15--36 μm ; ventral lobe broader, 0.62--0.8 times as wide as long; on soil and rocks, rarely xylicolous.
9. Leaves upturned; marginal cells distinctly smaller than median. Usually on soil . .25. *Scapania zemliae* (in part)
9. Leaves not upturned; marginal cells almost not differentiated from median in size. On rocks, and decaying wood, occasionally on soil.23. *Scapania mucronata* (in part)
4. Marginal cells of mature non-gemmiparous leaves more thick-walled than median cells.
10. Ventral lobe broader, 0.6--0.95 times as wide as long; purple pigmentation of leaves occurs sporadically; gemmae green, red or brown; on soil.
11. Marginal cells distinctly smaller than median in size; dorsal lobe triangular and sharp pointed to mucronate at apex; purple pigmentation of leaves absent; gemmae common, mostly red or brown in sun25. *Scapania zemliae* (in part)
11. Marginal cells hardly different from median in size; dorsal lobe rounded in blunt to mucronate apex; purple pigmentation of leaves frequent, at least near bases of ventral lobes; gemmae sporadic, green, sometimes reddish in sun27. *Scapania curta* (in part)
10. Ventral lobe more narrow, 0.45--0.6 (--0.7) times as wide as long, never purplish; gemmae reddish brown; mostly xylicolous, occasionally on sandstone and rocks.
12. Specialized asexual reproduction by gemmae mainly 1-celled at maturity; marginal leaf cells subsodiametric to tangentially elongated.35. *Scapania carinthiaca*
12. The majority of gemmae 2-celled at maturity; marginal leaf cells mostly subsodiametric34. *Scapania glaucocephala*
1. Keel acute from base to sinus or absent.
13. Keel uniformly less than 0.05 times the length of ventral lobe or absent . .12. *Scapania ornithopoides*
13. Keel usually more than 0.05 times the length of ventral lobe.
14. Ventral lobe decurrent proximal to keel insertion.
15. Marginal teeth spreading to bases of one or both lobes.
16. Terminal tooth cell slightly elongated, mostly to 1.5(--1.8) as long as wide.
17. Keel broadly winged, often dentate; dorsal lobe base never with branched teeth; purple pigmentation of ventral leaf base common; perianth mouth dentate like leaf margin15. *Scapania undulata* (in part)
17. Keel narrowly winged and entire in American plants; dorsal lobe base mostly with branched teeth; purple pigmentation absent; perianth mouth lobulate-dentate . . .4. *Scapania bolanderi* (in part)

16. Terminal tooth cell slender, mostly over 1.8 times as long as wide.
18. Keel moderately to strongly arched, wing more or less broad, often dentate . . .
15. *Scapania spitsbergensis*
18. Keel indistinctly to moderately arched, wing narrow, entire . .13. *Scapania americana*
15. Marginal teeth not spreading to lobe bases or absent.
19. Dorsal lobe (0.3--0.65--0.95 times the size of ventral lobe; cuticle coarsely to slightly papillose (if dorsal lobe 0.3--0.65 times the size of the ventral, cuticle coarsely papillose).
20. Cuticle coarsely papillose.
21. Dorsal lobe 0.3--0.75 times the size of the ventral5. **Scapania aspera*
21. Dorsal lobe 0.75--0.95 times the size of the ventral.
22. Lobes 0.9--1.1 times as wide as long , strongly turned backward; trigones mostly large, nodose11. *Scapania simmonsii* (in part)
22. Lobes 0.5--0.8 times as wide as long, stiffly spread from each other; trigones mostly small, acute to slightly bulging22. *Scapania hians*
20. Cuticle moderately to slightly papillose.
23. Leaves strongly turned backward; dorsal lobe 0.75--0.95 times the size of the ventral11. *Scapania simmonsii* (in part)
23. Leaves never strongly turned backward; dorsal lobe 0.65--0.8 times the size of the ventral.
24. Leaves invariably entire; keel wing absent; secondary pigmentation fuscous17. *Scapania obscura* (in part)
24. Leaves dentate; keel wing narrow; secondary pigmentation red to brown.
25. Median cells with small acute trigones; marginal cells mostly thick-walled, sporadically thin-walled, 16--22 μm where subsodiametric16. *Scapania subalpina*
25. Median cells with bulging trigones; marginal cells mostly thin-walled, 20--26(--28) μm where subsodiametric19. *Scapania serrulata*
19. Dorsal lobe 0.25-- 0.65(--0.7) times the size of the ventral; cuticle never coarsely papillose.
26. Dorsal lobe subparallel to stem; keel moderately to strongly arched, shorter, (0.05--0.15--0.35 times the size of ventral lobe 20. *Scapania uliginosa*
26. Dorsal lobe divergent with stem; keel indistinctly to moderately arched, longer, 0.25--0.55 times the size of ventral lobe.
27. Terminal tooth cell 2--3 times as long as wide; gemmae common, 1-celled, brown3. *Scapania nemorea*
27. Terminal tooth cell to 1.5 times as long as wide; gemmae sporadic to common, 2-celled, green to purple in sun or reddish brown.

28. Lobes broadly rounded to weakly pointed at apex; gemmae broadly ovoid, 10--17 x 12--23 μm , green to purplish in sun; median cells with indistinct to moderate acute trigones; larger, 15--200 x 1.5--4.5 mm.

.15. *Scapania undulata* (in part)

28. Lobes triangular and sharply pointed at apex; gemmae bacilliform to narrowly ovoid, 7--11 x 15--27 μm , reddish brown; median cells with moderate acute to bulging trigones; smaller, 5--20 x 0.5--2.5 mm.1.

Scapania umbrosa (in part)

[[MOVED 14B. TO LEFT]]

14. Ventral lobe subtransversely inserted or decurrent to keel insertion.

29. Dorsal lobe 0.75--0.95 times the size of ventral.

30. Leaves incurved and upturned; monoicous37. *Scapania kaurinii* (in part)

30. Leaves never incurved and upturned; dioicous and monoicous.

31. Cuticle coarsely papillose; dioicous; perianth mouth lobulate-dentate
.6. * *Scapania aequiloba*

31. Cuticle slightly to moderately papillose; monoicous and dioicous; perianth mouth entire to dentate7. *Scapania compacta* (in part)

29. Dorsal lobe less than 0.75 times the size of ventral.

32. Branched teeth common near dorsal lobe base4. *Scapania bolanderi* (in part)

32. Teeth absent basally.

33. Ventral lobe mostly more than 0.85 times as wide as long.

34. Specialized asexual reproduction by gemmae usually present, mostly or entirely 1-celled; oil bodies usually persistent2. *Scapania brevicaulis* (in part)

34. Specialized asexual reproduction by gemmae unknown or occasionally present, mostly 2-celled; oil bodies usually not persistent/

35. Marginal cells more or less thick-walled; plants green to slightly brownish; gemmae unknown14. *Scapania hollandiae* (in part)

35. Marginal cells thin-walled; plants usually more or less brown to green or sometimes reddish or purplish-brown; gemmae occasionally present.

36. Dorsal lobe decurrent, extending far beyond stem, subparallel to slightly divergent with it33. *Scapania paludicola*

36. Dorsal lobe not decurrent, not or slightly extending beyond stem, divergent with it.

37. Keel wing mostly absent or indistinct.

38. Dorsal lobe 0.5--0.75(--0.8) times the size of ventral; gemmae broadly ovoid, 10--21 x 12--31(--33) μm , green to brown and purple; median cells with mostly bulging trigones32. *Scapania hyperborea*

38. Dorsal lobe 0.5--0.6 times the size of ventral; gemmae narrowly ovoid, 9--12 x 20--28 μm , green; median cells with acute to bulging trigones .31. *Scapania irrigua*

37. Keel with mostly distinct, narrow to rarely broad wing.

39. Paroicous; leaves mostly upturned and incurved; keel wing narrow; trigones small to slightly bulging.37. *Scapania kaurinii* (in part)

39. Dioicous; leaves rarely upturned and incurved; keel wing narrow or rarely broad; trigones moderate to strongly bulging.
40. Leaf margin mostly irregularly dentate distally; keel wing more or less broad, often dentate; marginal cells large, 23--32 μm where subsodiametric; gemmae broadly ovoid, green to purple and brown.32. *Scapania hyperborea*
40. Leaf margin denticulate distally to entire; keel wing more or less narrow, entire; marginal cells smaller, 15--20 μm where subsodiametric; gemmae mostly elliptical-fusiform, brown2. *Scapania brevicaulis* (in part)

[[MOVED 33B. TO LEFT]]

33. Ventral lobe mostly less than 0.85 times as wide as long.
41. Mature gemmae 1-celled, common.
42. Specialized asexual reproduction by gemmae green30. *Scapania fulfordiae*
42. Specialized asexual reproduction by gemmae pigmented, red or brown.
43. Oil bodies persistent; median cells with small acute to moderate bulging trigones; on soil2. *Scapania brevicaulis* (in part)
43. Oil bodies not persistent; median cells with large bulging to moderate acute trigones; xylicolous36. *Scapania apiculata*
41. Mature gemmae 2-celled, common, sporadic or unknown.
44. Marginal sector of ventral lobe base hyaline, without oil bodies and chloroplasts; oil bodies persistent; gemmae common.
45. Specialized asexual reproduction by gemmae more narrow and short, 12--17 x 20--32 μm ; marginal cells thin-walled10. *Scapania gymnostomophila*
45. Specialized asexual reproduction by gemmae usually broader and longer, (14--16--24 x 25--40 μm ; marginal cells thick- to thin-walled.
46. Leaves entire to crenulate-denticulate (usually a few leaves with isolated teeth on every plant); gemmae green to brownish; perianth mouth subentire to denticulate8. *Scapania pseudocalcicola*
46. Leaves (except female bracts) entire; gemmae yellowish to deep brown or reddish brown; perianth mouth lacinate-dentate9. *Scapania ligulifolia*
44. Marginal sector of ventral lobe base not hyaline, with oil bodies and chloroplasts; oil bodies not persistent; gemmae frequent or unknown.
47. Marginal leaf cells thick-walled.
48. Dorsal lobe extending to far edge and often beyond stem; purple pigmentation absent; plants larger, 1.8--4.5 mm wide14. *Scapania hollandiae* (in part)
48. Dorsal lobe not extending to far edge of stem; purple pigmentation frequent; plants smaller, 1--2.5(--3) mm wide.
49. Dorsal lobe distinctly divergent with stem; keel longer, 0.45--0.7 times the length of ventral lobe.
50. Leaves entire to denticulate distally; dorsal lobe 0.5--0.85 times the size of ventral, rounded in blunt to mucronate apex; gemmae more or less narrowly ovoid27. *Scapania curta* (in part)
50. Leaves mostly denticulate to irregularly coarsely dentate distally; dorsal lobe 0.4--0.75 times the size of ventral, more or less triangular and pointed in

- apiculate to mucronate apex; gemmae variable in shape, from narrowly elliptic to broadly ovoid and obtusely angulate26. *Scapania lingulata* (in part)
49. Dorsal lobe subparallel to slightly divergent with stem; keel shorter, 0.25--0.5 times the length of ventral lobe.
51. Specialized asexual reproduction by gemmae reddish brown, bacilliform to narrowly ovoid, 7--11 x 15--27 μm 1. *Scapania umbrosa* (in part)
51. Specialized asexual reproduction by gemmae green, more or less narrowly ovoid, 7--13 x 18--25 μm . . .5. *Scapania scandica* (in part)
47. Marginal leaf cells thin-walled.
52. Leaves usually incurved and upturned; paroicous. . . .37. *Scapania kaurinii* (in part)
52. Leaves not incurved and upturned; dioicous.
53. Dorsal lobe subparallel to slightly divergent with stem; keel shorter, 0.25--0.5 times the length of ventral lobe.
54. Specialized asexual reproduction by gemmae, reddish brown, bacilliform to narrowly ovoid, 7--11 x 15--27 μm 1. *Scapania umbrosa* (in part)
54. Specialized asexual reproduction by gemmae, green, more or less narrowly ovoid, 7--13 x 18--25 μm . . .29. *Scapania scandica* (in part)
53. Dorsal lobe distinctly divergent with stem; keel longer, 0.5--0.7 times the length of ventral lobe.
55. Marginal cells larger, 18--28 μm where subisodiametric.
56. Leaves entire to denticulate distally; dorsal lobe 0.5--0.85 times the size of ventral, rounded in blunt to mucronate apex; gemmae more or less narrowly ovoid27. *Scapania curta* (in part)
56. Leaves mostly denticulate to irregularly coarsely dentate distally; dorsal lobe 0.4--0.75 times the size of ventral, more or less triangular and pointed in apiculate to mucronate apex; gemmae variable in shape, from narrowly elliptic to broadly ovoid and obtusely angulate26. *Scapania lingulata* (in part)
55. Marginal cells smaller, 14--19 μm where subisodiametric.
57. Dorsal lobe of mature leaves blunt to rounded at apex . . .7. **Scapania helvetica*
57. Dorsal lobe of mature leaves apiculate to mucronate at apex .23. *Scapania mucronata* (in part)

1. *Scapania umbrosa* (Schrad.) Dumortier, Recueil Observ. Jungerm. 14. 1835

Jungermannia umbrosa Schrad., Syst. Samml. Krypt. Gew. (2): 5. 1797

Plants 5--20 x 0.5--2.5 mm, green to reddish brown. **Leaves** usually more or less serrate distally, terminal tooth cell to 1.5 times as long as wide; dorsal lobe 0.5 times the size of ventral, 0.5--0.7 times as wide as long, subtransversely inserted, not extending to far edge of stem, subparallel to slightly divergent, usually triangular and sharply pointed at apex; ventral lobe 0.45--0.65 times as wide as long, decurrent proximal to keel insertion to arcuately inserted, usually

triangular and sharply pointed at apex, not hyaline near base margin; keel 0.25--0.45 times the length of ventral lobe, acute, indistinctly arched, wing often narrow, entire. **Median leaf cells** with moderate acute to bulging trigones; marginal cells often thick-walled, 14--19 μm where subisodiametric; oil bodies not persistent; cuticle moderately papillose. **Specialized asexual reproduction** by gemmae, frequent, reddish brown, 2-celled, bacilliform to narrowly ovoid, 7--11 x 15--27 μm . **Sexual condition** dioicous. **Perianth** strongly compressed, mouth entire.

Rotten wood and wet rocks in places with perpetually high atmospheric humidity in non-Arctic areas mostly of the eastern and western coasts; 0--1200 m; St. Pierre and Miquelon; B.C., N.B., Nfld., N.S., Ont., Que.; Alaska, Calif., Idaho, Maine, Mont., N.H., N.Y., Oreg., Wash., Wis.; Europe; Asia (Turkey, South Siberia, Sakhalin, Kamchatka); Atlantic Islands.

There are no records of *Scapania umbrosa* for P.E.I. although the species may be expected to occur there. The most distinctive character of *Scapania umbrosa* is unique in *Scapania*, being bacilliform to narrowly ovoid, reddish brown gemmae. The species is exceedingly variable in the degree of ventral lobe decurrency, leaf dentition, and intensity of gemma production. Poor development of gemmae or their absence may result in confusion of *S. umbrosa* with *S. scandica* and with small forms of *S. undulata*. In such cases a complex analysis of characters and of their correlative variability is important. Non-gemmiparous *S. umbrosa* is usually distinct from *S. scandica* in leaf lobes being weakly divergent with each other and from small forms of *S. undulata* in more or less gradually triangular and sharply pointed lobe apices (vs. more or less rounded lobe apices).

2. *Scapania brevicaulis* Taylor, London J. Bot. 5: 272. 1846

Scapania arnellii Buch; *S. degenii* Schiffner ex K. Müller (Freiburg); *Scapania degenii* var. *dubia* R. M. Schuster

Plants 5--50 x (0.5--0.8--4 mm, green to fuscous, rarely purplish postically. **Leaves** entire to dentate distally, terminal tooth cell to 1.5 times as long as wide; dorsal lobe 0.5--0.75 times the size of ventral, 0.5--1.4 times as wide as long, subtransversely inserted, sometimes extending to far edge of stem or slightly beyond it, divergent with stem, obtusely to acutely pointed; ventral lobe 0.45--1(--1.12) times as wide as long, arcuately to subtransversely inserted, rounded to mucronate at apex, not hyaline near base margin; keel 0.3--0.65 times the length of ventral lobe, acute, indistinctly to strongly arched, wing narrow in robust forms, entire. **Median leaf cells** with small acute to moderate bulging trigones; marginal cells not differentiated, 15--20 μm where subisodiametric; oil bodies mostly persistent; cuticle slightly to moderately papillose. **Specialized asexual reproduction** by gemmae usually present, brown, 1(--2)-celled, mostly elliptical-fusiform, 10--16(--18) x 12--25(--28) μm . **Sexual condition** dioicous. **Perianth** more or less compressed, mouth shortly dentate to entire.

Tundra and alpine communities, mostly on slightly calcareous soil; 0--3000 m; Greenland; Alta., B.C., Man., Nfld., N.W.T., Ont., Que.; Alaska, Colo., Minn., Mont., N.H.; Eurasia.

There are no records of *Scapania brevicaulis* for the Yukon although the species may be expected to occur there. The elevational range of *S. brevicaulis* is incompletely known. Problems

of differentiation of *S. brevicaulis* are considered under *S. hyperborea* and *S. carinthiaca*. It may also be confused with *S. nemorea* subsp. *crassiretis*. Main distinctions from the latter are ventral lobes decurrent to keel insertion; moderately to strongly arched keel of robust plants (vs. indistinctly arched keel); at most moderate bulging (vs. large bulging) trigones; slightly elongated (to 1.5 times as long as wide) terminal tooth cells; and usual absence of purple pigmentation of ventral lobe bases (vs. usual presence of it). The leaves of *S. brevicaulis* are occasionally upturned. The synonymy of *S. brevicaulis* follows A. D. Potemkin (1999). Its robust broad leaved and most common phenotypes were previously treated as *S. degenii*.

3. *Scapania nemorea* (Linneaus) Grolle, Rev. Bryol. Lichenol.32: 160. 1963

Jungermannia nemorea Linneaus, Syst. nat. (ed.10) 2: 1337. 1759; *Scapania nemorosa* (Linneaus) Dumortier

Plants 10--100 x 1.2--5.5 mm, green to fuscous and purplish brown. **Leaves** dentate distally, terminal tooth cell 2--3 times as long as wide; dorsal lobe 0.25--0.7 times the size of ventral, 0.8--1.4 times as wide as long, decurrent to arcuately inserted, extending to far edge of stem or slightly beyond it, divergent with stem, apiculate to bluntly pointed at apex; ventral lobe 0.55--1(--1.1) times as wide as long, decurrent proximal to keel insertion, broadly rounded to bluntly pointed at apex, not hyaline near base margin; keel 0.25--0.55 times the length of the length of the ventral lobe, acute, indistinctly to moderately arched, wing narrow to broad, rarely dentate. **Median leaf cells** with small acute to large bulging trigones; marginal cells often thick-walled, 10--20 μ m where subisodiametric; oil bodies occasionally persistent; cuticle moderately papillose. **Specialized asexual reproduction** by gemmae, common, brown, almost invariably 1-celled, ellipsoid, (7--)8--13 x 12--22 μ m. **Sexual condition** dioicous. **Perianth** compressed, mouth dentate-ciliate to sparsely dentate and entire.

Subspecies 2 (2 in the flora): Greenland; Canada; United States; Eurasia; Atlantic Islands.

1. Dorsal lobe 0.25--0.5 times the size of ventral, mostly long-decurrent; leaves often coarsely dentate and then with teeth in distal parts of leaves mainly 2-celled at base; median leaf cells mostly with small to moderate trigones and non-persistent oil-bodies; perianth mouth dentate-ciliate to sparsely dentate. . . . 3a. *Scapania nemorea* subsp. *nemorea*

1. Dorsal lobe 0.4--0.7 times the size of ventral, arcuately inserted to short-decurrent; leaves usually slightly dentate, with slender 1--2(--3)-celled teeth 1-celled at base, or entire; median leaf cells with mostly large bulging trigones and persistent oil-bodies; perianth mouth sparsely dentate or entire. 3b. *Scapania nemorea* subsp. *crassiretis*

3a. *Scapania nemorea* (Linneaus) Grolle subsp. *nemorea*

Leaves often coarsely dentate and then with teeth in distal part of leaves mainly 2-celled at base; dorsal lobe 0.25--0.5 times the size of ventral, mostly long-decurrent. **Median leaf cells** usually with small acute to moderate, slightly bulging trigones; oil bodies mostly not persistent. **Perianths** common, mouth dentate-ciliate to sparsely dentate.

Exceedingly broad ecological amplitude, soil, rocks, decaying wood, bases of trees; 0--2000 m; Greenland?; St. Pierre and Miquelon; N.B., Nfld., N.S., Ont., Que.; Ala., Ark., Conn., Del., D.C., Fla., Ga., Ill., Ind., Iowa, Kans., Ky., La., Maine, Md., Mass., Mich., Minn., Miss., Mo., Nebr., N.H., N.J., N.Y., N.C., Ohio, Okla., Pa., R. I., S. C., Tenn., Tex., Vt., Va., W. Va., Wis.; Europe; Asia (Turkey); Atlantic Islands.

There are no records of *Scapania nemorea* subsp. *nemorea* for P.E.I. although the subspecies may be expected to occur there. The known Greenland material is certainly *S. nemorea*. It was found in Plantae Groenlandicae a Museo botanico Hauensi distributae as not well developed *S. gracilis* Lindb.; the collector and locality were not mentioned, but the specimen was annotated by R. M. Schuster in July 1954 as *S. nemorosa*. I, as well as R. M. Schuster (1974: 581), who cited no Greenland collection for *S. nemorosa*, doubt if the label corresponds to the specimen. Despite rather many reports of this subspecies from the Arctic, no identification has been confirmed. Distinction of *S. nemorea* subsp. *nemorea* from *S. undulata* is discussed under the latter taxon.

3b. *Scapania nemorea* subsp. *crassiretis* (Bryhn) Potemkin, J. Hattori Bot. Lab. 77: 277. 1994

Scapania crassiretis Bryhn, Rev. Bryol. 19: 7. 1892

Leaves slightly dentate, with slender 1--2(--3)-celled teeth 1-celled at base; dorsal lobe 0.4--0.7 times the size of ventral, arcuately inserted to short-decurrent. **Median leaf cells** with mostly large bulging trigones; oil bodies often persistent. **Perianths** rare, mouth sparsely dentate to entire.

Rocks and soil in the Arctic, spreading southward in mountains of Europe and East Siberia; 0--2000 m; Greenland; N.W.T., Que., Yukon; Alaska; Eurasia.

Scapania nemorea subsp. *crassiretis* may be confused with robust forms of *S. brevicaulis* (known as *S. degenii*). Their distinction is considered under *S. brevicaulis*. There is some similarity with *S. simmonsii* as well. The last, however, never produces gemmae, has larger dorsal lobes, slightly elongated terminal tooth cells, no purple pigmentation, a moderately arched keel, and often has a coarsely papillose cuticle. On the basis of molecular studies by Vilnet et al., (2010) and J. Heinrichs et al. (2012) this subspecies is treated as a separate species *Scapania crassiretis*.

4. *Scapania bolanderi* Austin, Proc. Acad. Nat. Sci. Philadelphia (1869) 21: 218. 1870

Scapania granulifera Evans

Plants 10--50 x 1.5--3.5 mm, green to brown. **Leaves** dentate basally, near dorsal lobe base particularly, basal teeth often branched, terminal tooth cell 1.3--1.8 times as long as wide; dorsal lobe 0.3--0.6(--0.75) times the size of ventral, 0.85--1.1 times as wide as long, arcuately inserted, extending to far edge of stem or slightly beyond it, divergent with it, sharply to obtusely pointed at apex; ventral lobe 0.5--0.75 times as wide as long, decurrent to or proximal to keel insertion, rounded to triangular and pointed at apex, not hyaline near base; keel 0.2--0.35 times the length

of ventral lobe, acute, indistinctly arched, wing normally narrow, entire. **Median leaf cells** with moderate acute to bulging trigones; marginal cells thick- to thin-walled, 10--18 μm where subisodiametric; oil bodies often persistent; cuticle slightly to rather coarsely papillose.

Specialized asexual reproduction by gemmae sporadic, green, 2-celled, ellipsoid, 10--12 x 20--26 μm . **Sexual condition** dioicous. **Perianth** compressed, mouth lobulate-ciliate.

Rotten wood, bark of living trees, mainly gymnosperms, rarely also on soil in forested areas of western North America; 0--1500 m; B.C.; Alaska, Calif., Idaho, Oreg., Wash.; Asia (China, Japan, Russian Far East).

Scapania bolanderi is distinct from the other North American species of *Scapania* in its common development of branched teeth near the dorsal lobe base. Branched teeth infrequently occur near the dorsal lobe base of *S. spitsbergensis* and *S. ornithopoides*. The former, however, is distinct from *S. bolanderi* in paroicous sex distribution, common purple pigmentation and a keel with broad often dentate wing. The latter is isolated in its indistinct vestigial keel less than 0.05 times the length of the ventral lobe.

5. *Scapania aspera M. & H. Bernet, Bernet H., Cat. Hép. S.-O. Suisse 42. 1888

Plants 10--50 x 1.5--5 mm, green to brown and brownish purple. **Leaves** dentate distally, terminal tooth cell 1.3--2 times as long as wide; dorsal lobe 0.3--0.75 times the size of ventral, 0.8--1.4 times as wide as long, decurrent to arcuately inserted, extending to far edge of stem or slightly beyond it, divergent with stem, pointed to almost cuspidate at apex; ventral lobe 0.6--0.9 times as wide as long, decurrent proximal to keel insertion, rounded to mucronate at apex, not hyaline near base margin; keel 0.3--0.65 times the length of ventral lobe, acute, indistinctly to moderately arched, wing occasionally narrow, entire. **Median leaf cells** with small to moderate acute, rarely bulging trigones; marginal cells more or less thick-walled, 12--20 μm where subisodiametric; oil bodies occasionally persistent; cuticle more or less coarsely papillose. **Specialized asexual reproduction** by gemmae sporadic, green, 2-celled, ovoid to slightly angulate, 14--20 x 19--40 μm . **Sexual condition** dioicous. **Perianth** moderately compressed, mouth lobulate-dentate.

Habitats, elevation, and distribution of *Scapania aspera* in the area of the flora remain unclear; Nunavut (Baffin Island).

Mostly on calcareous soil and rocks in Europe; altitudinal range outside the territory of the flora 0--1500 m; range outside the territory of the flora; Europe; Asia (Turkey, SE China).

The only report of *Scapania aspera* for North America, from Baffin I. (N. Polunin 1947: 509), is based on identification by W. R. Sherrin, and is doubtful (R. M. Schuster 1974: 612). The specimen was unavailable for study. Recent finds of *S. aspera* in the northern East Siberia (E. Borovichev et al., 2016 unpublished; <http://kpabg.ru/h/?q=node/41912>) point out that its range is still imperfectly known and imply a possibility of its occurrence in northern North America. *Scapania aspera* may be confused there with *S. americana* from which the former differs in its entire ventral lobe base, coarsely papillose cuticle, less elongated terminal tooth cell (1.3--2.0 vs. 1.8--2.2 times as long as wide), and calciphilous ecology.

6. **Scapania aequiloba* (Schwägrichen) Dumortier, Recueil Observ. Jungerm., 14. 1835

Jungermannia aequiloba Schwägrichen, Hist. Musc. Hep. Prodr., 24. 1814

Plants 10--50 x 1.5--3 mm, green to brown. **Leaves** dentate distally, terminal tooth cell to 1.5 times as long as wide; dorsal lobe 0.75--0.95 times the size of ventral, 0.6--1.0 times as wide as long, arcuately inserted, extending to far edge of stem or slightly beyond it, divergent with stem, triangular and pointed at apex; ventral lobe 0.55--0.8 times as wide as long, arcuately inserted, triangular and pointed at apex, not hyaline near base margin; keel 0.5--0.75 times the length of ventral lobe, acute, indistinctly to moderately arched, wing occasionally narrow, entire. **Median leaf cells** with moderate, mostly acute trigones; marginal cells thick-walled, 10--16 μm where subisodiametric; oil bodies occasionally persistent; cuticle coarsely papillose. **Specialized asexual reproduction** by gemmae sporadic, green, 2-celled, ovoid to slightly angulate, 10--17 x 20--30 μm . **Sexual condition** dioicous. **Perianth** moderately compressed, mouth lobulate-dentate.

Habitats, elevation, and distribution of *Scapania aequiloba* in the range of the flora remain to be unclear; Greenland; Nunavut (Ellesmere Island); Europe; Asia (Turkey).

Scapania aequiloba has been reported from Ellesmere Isl. (N. Bryhn 1906) and W. Greenland (K. Müller 1951--1958). Reports of this basically temperate and warm-temperate *S. aequiloba* from the high Arctic are extremely doubtful. Found among Mitten's collections at NY, the specimen of rather typical *S. aequiloba*, labeled "NW America, Plover Bay." This is virtually the only reason to keep the species in the Flora. Outside the territory of the flora the species occurs on calcareous soil and rocks, occasionally on rotten wood; to 2600 m. The leaves of *S. aequiloba* have lobes mostly stiffly spreading from each other.

7. *Scapania compacta* (A. W. Roth) Dumortier, Recueil Observ. Jungerm. 14. 1835

Jungermannia compacta A. W. Roth, Tentam. Fl. Germ. 375. 1800

Plants 3--50 x 1.2--4 mm, green to brown. **Leaves** entire to denticulate distally; dorsal lobe 0.75--0.95 times the size of ventral, 0.55--1.2 times as wide as long, subtransversely inserted, often extending to far edge of stem and occasionally beyond it, divergent with stem, rounded to obtusely pointed at apex; ventral lobe 0.6--1.2 times as wide as long, arcuately inserted, rounded to obtusely pointed at apex, not hyaline near base margin; keel 0.5--0.75 times the length of ventral lobe, rounded to subacute basally, acute near sinus, indistinctly arched, wing absent. **Median leaf cells** with small acute to moderate slightly bulging trigones; marginal cells not differentiated, 15--20 μm where subisodiametric; oil bodies occasionally persistent; cuticle slightly to moderately papillose. **Specialized asexual reproduction** by gemmae sporadic, green to brown, 2-celled, broadly ovoid, 16--21 x 23--32 μm . **Sexual condition** monoicous and dioicous. **Perianth** mostly compressed, mouth entire to dentate.

Stream alluvium; 50 m; Alaska; Europe: Asia (Turkey); Africa; Atlantic Islands.

Scapania compacta is exceedingly variable in lobe width/length ratio, keel expression and perianth compression. Common forms are rather robust and have dorsal lobes suberect and extending to the far edge of the stem and occasionally beyond it, but the ventral lobe is turned backward; the keel is usually rounded basally and acute near the sinus only; and the perianth is strongly compressed. Such plants may be confused with forms of *S. hyperborea* with large dorsal lobes. They differ from the latter in frequent monoicous sex distribution, specific orientation of lobes with respect to each other, inability to produce large bulging trigones and purple gemmae. Sporadic occurrence of rather small narrow-leaved forms with dorsal lobes not crossing the stem and variable perianth compression (K. Damsholt and D. Long 1981; A. D. Potemkin 1995) makes differentiation of *S. compacta* from *S. obcordata* problematic. Such forms are easy to distinguish from *S. obcordata* when monoicous sexuality is obvious. They may be distinct also from *S. obcordata* in the ability to produce distinct trigones of leaf cells, absence of purple pigmentation of leaves and gemmae, slightly saccate male bracts, and female bracts usually larger than adjacent sterile leaves. The leaves of *S. compacta* have lobes mostly spreading from each other.

8. *Scapania pseudocalcicola* Schuster, Phytologia 63: 327. 1987

Plants 10--30 x 1--3(--4) mm, green to brownish. **Leaves** entire to crenulate-denticulate distally; dorsal lobe 0.5--0.65 times the size of ventral, (0.45--0.6--0.95 times as wide as long, subtransversely inserted, not extending to far edge of stem, divergent with it, sharply to bluntly pointed at apex; ventral lobe (0.45--0.55--0.8 times as wide as long, arcuately inserted, sharply pointed at apex, hyaline near base margin; keel (0.4--0.5--0.65 times the length of ventral lobe, acute, indistinctly arched, wing locally narrow, entire. **Median leaf cells** with small acute to moderate slightly bulging trigones; marginal cells thick- to thin-walled, 17--23 μ m where subisodiametric; oil bodies persistent; cuticle slightly papillose. **Specialized asexual reproduction** by gemmae, common, green to brownish, 2-celled, ovoid to slightly angulate, 15--21 x 24--40 μ m. **Sexual condition** dioicous. **Perianth** inflated, mouth denticulate to subentire.

Calcareous soil and rocks in the Atlantic Arctic and subarctic; of conservation concern; 0--200 m; Greenland; Nfld., Que.

Scapania pseudocalcicola without perianths appears similar to *S. ligulifolia*. It differs from the latter in the occurrence of small denticulations in distal parts of at least some leaves and in the usually green to brownish (vs. yellow to brown) gemmae in sun forms. Many specimens labeled *Scapania calcicola* are this species. The leaves of *S. pseudocalcicola* are usually upturned.

9. *Scapania ligulifolia* R. M. Schuster, Hepat. Anthocerotae N. Amer. 3: 306, f. 355. 1974

Scapania calcicola var. *ligulifolia* R. M. Schuster [heterotypic]

Plants 3--18 x 0.8--2.4(--2.7) mm, green to brown. **Leaves** entire; dorsal lobe 0.4--0.65 times the size of ventral, 0.7--1.1 times as wide as long, subtransversely inserted, not extending to far edge of stem, divergent with it, bluntly to sharply pointed at apex; ventral lobe 0.65--0.77 times as wide as long, arcuately inserted, obtusely to sharply apiculate at apex, hyaline near base

margin; keel 0.45--0.6 times the length of ventral lobe, acute, indistinctly to moderately arched, wing occasionally narrow, entire. **Median leaf cells** with small acute to moderate bulging trigones; marginal cells thick- to thin-walled, 15--19(--24) μm where subisodiametric; oil bodies persistent; cuticle slightly papillose. **Specialized asexual reproduction** by gemmae, common, yellowish (rarely reddish) to deep brown, 2-celled, ovoid to slightly angulate, 14--23 x 25--40 μm . **Sexual condition** dioicous. **Perianth** inflated, mouth laciniate-dentate.

Calcareous rocks and soil in the Arctic; 0--200 m; Greenland; N.W.T., Que.; Europe (Svalbard, Franz-Josef Land); Asia (n Russia).

Scapania ligulifolia without perianths may be confused with *S. pseudocalcicola*. Their distinction is considered under the latter species. The leaves of *S. ligulifolia* are more or less upturned and incurved.

10. *Scapania gymnostomophila* Kaalaas, Bot. Not. 1896: 21. 1896

Diplophyllum incurvum Bryhn & Kaalaas

Plants 3--16(--20) x 0.7--2.4 mm, green to brown. **Leaves** entire; dorsal lobe 0.25--0.65 times the size of ventral, 0.5--0.75 times as wide as long, subtransversely inserted, not extending to far edge of stem, divergent with it, triangular and pointed to obtuse at apex; ventral lobe 0.5--0.8 times as wide as long, arcuately inserted, pointed to rounded at apex, hyaline near base margin; keel 0.35--0.5 times the length of ventral lobe, acute, indistinctly to moderately arched, wing often narrow, entire. **Median leaf cells** with small trigones; marginal cells not differentiated, 10--15 μm where subisodiametric; oil bodies persistent; cuticle slightly papillose. **Specialized asexual reproduction** by gemmae, common, brown to reddish brown, 2-celled, ovoid to rhomboid, 12--17 x 20--32 μm . **Sexual condition** dioicous. **Perianth** inflated, mouth lobulate-to fimbriate-ciliate.

Calcareous soil and rocks; 0--2500 m; Greenland; B.C., Nfld., N.W.T., [[Nun.??]] N.S., Ont., Que., Yukon; Alaska, Idaho, Maine, Mass., Mich., Minn., Mont., N.Y., Vt., Wis.; Eurasia.

The elevational range of *Scapania gymnostomophila* in the territory of the flora is imperfectly known. In Europe the species has been found at up to 2650 m. *Scapania gymnostomophila* is distinct from all other *Scapania* in having large plate-like brown persistent oil bodies occurring mostly 1 per cell. In addition, it may be distinguished from the similar *S. pseudocalcicola* and *S. calcicola* by smaller gemmae and entire, invariably unbordered leaves. The leaves of *S. gymnostomophila* are often upturned and incurved.

11. *Scapania simmonsii* Bryhn & Kaalaas, Report 2nd Norw. Arct. Exped. Fram. 2(11): 51. 1906

Plants 10--60 x (1.5--2.5--3 mm, fuscous. **Leaves** dentate distally, terminal tooth cell to 1.5 times as long as wide; dorsal lobe convex, 0.75--0.95 times the size of ventral, 0.9--1.1 times as wide as long, decurrent, extending beyond stem, divergent with it, triangular and pointed to obtuse and rounded at apex; ventral lobe convex and strongly recurved, 0.9--1.1 times as wide

as long, decurrent proximal to keel insertion, triangular and pointed to obtuse and rounded at apex, not hyaline near base margin; keel 0.25--0.5 times the length of ventral lobe, acute, moderately arched, wing mostly absent. **Median leaf cells** with mainly large bulging trigones; marginal cells thin- to thick-walled, 18--23 μm where subsodiametric; oil bodies occasionally persistent; cuticle moderately to coarsely papillose. **Specialized asexual reproduction** by gemmae unknown. **Sexual condition** dioicous. **Perianth** compressed, mouth lobulate-ciliate.

Mostly on calcareous soil in the Arctic; 0--500 m; Greenland; N.W.T., Que., Yukon; Alaska; Europe (n Russia, Svalbard); Asia (n Russia).

Scapania simmonsii is a well-defined species due to strongly turned backward leaves with subequal lobes about as wide as long and normally very coarse trigones. It may be mistaken only for *S. crassiretis*. The leaves are strongly turned backward.

12. *Scapania ornithopoides* (Withering) Waddell, Moss Exchange Club Cat. Brit. Hep., 4. 1897 "ornithopodioides"

Jungermannia ornithopoides Withering, Bot. Arr. Veg. Great Britain 2: 695. 1776

Plants 30--150 x 1.5--4.5 mm, brown to reddish brown. **Leaves** dentate-ciliate from apex to base, terminal tooth cell 2--4 times as long as wide; dorsal lobe mostly 0.35--0.6 times the size of ventral, 0.75--1.1 times as wide as long, arcuately inserted to short-decurrent, extending beyond stem, subparallel to divergent with it, sharply pointed to obtuse at apex; ventral lobe 0.55--0.85 times as wide as long, decurrent to or proximal to keel insertion, rounded to sharply pointed at apex, not hyaline near base margin; keel absent or less than 0.05 times the length of ventral lobe, acute, more or less strongly arched, wing broad, dentate. **Median leaf cells** with mainly large bulging trigones; marginal cells mostly not differentiated, 14--20 μm where subsodiametric; oil bodies largely not persistent; cuticle smooth to coarsely papillose. **Specialized asexual reproduction** by gemmae rare (unknown for North American plants) brown to purple, 1--2-celled, broadly ellipsoid, 17--21 x 20--28 μm . **Sexual condition** dioicous. **Perianth** strongly compressed, mouth lobulate-dentate.

Usually on peaty wetland slopes and cliff terraces at higher elevations; confined to very oceanic climates of Pacific Islands and oceanic territories of the North Pacific Coast from Queen Charlotte Island to Aleutian Islands; 0--500 m; B.C.; Alaska; Europe (Great Britain, Faroes, Ireland, Norway); Asia (Assam, Bhutan, China, Darjeeling, Japan, Nepal, Sikkim, Taiwan); Pacific Islands (Hawaii, Philippines).

Scapania ornithopoides is distinct from the other North American species of *Scapania* in its invariably vestigial keel less than 0.05 times the length of the ventral lobe. Distinction from forms of *S. uliginosa* with very short keels are considered under that species. According to Art. 60.1 of International Code of Nomenclature for algae, fungi, and plants (Melbourne Code) (2012), the species epithet of *Scapania ornithopoides* must be given the original spelling of W. Withering (1776).

13. *Scapania americana* K. Müller (Freiburg), Bull. Herb. Boissier (ser.2) 3: 44. 1903 [1902] E

Scapania bolanderi var. *americana* (K. Müller (Freiburg)) Frye & Clark

Plants 10--30 x 1.5--3.5 mm, green to brown and purplish. **Leaves** dentate at least to postical leaf bases, terminal tooth cell mostly 1.8--2.2 times as long as wide; dorsal lobe 0.4--0.75 times the size of ventral, 1--1.3 times as wide as long, arcuately inserted or decurrent, extending beyond stem, divergent with it, rounded to sharply pointed at apex; ventral lobe 0.55--0.75 times as wide as long, decurrent proximal to keel insertion, mostly rounded to blunt at apex, not hyaline near base margin; keel 0.35--0.56 times the length of ventral lobe, acute, indistinctly to moderately arched, wing mostly absent. **Median leaf cells** with small acute to moderate bulging trigones; marginal cells thick- to thin-walled, 9--17(--20) μm where subisodiametric; oil bodies not persistent; cuticle smooth to moderately papillose. **Specialized asexual reproduction** by gemmae sporadic, deep purple to brownish, (1--2)-celled, broadly ellipsoid to ovoid, 12--16 x 15--26 μm . **Sexual condition** dioicous. **Perianth** strongly compressed, mouth lobulate-ciliate to dentate.

Generally on rocks in shaded sites of forested areas; 0--1500 m; Alta., B.C., N.W.T.; Alaska, Calif., Idaho, Mont., Oreg., Wash.

Scapania americana is frequently confused with *S. bolanderi*. It is distinct from the latter in slender teeth with spinose terminal cells, lacking branched marginal teeth spread primarily to the ventral lobe base, bearing pigmented gemmae, and in its saxicolous ecology. Forms of *S. americana* with large dorsal lobes resemble *S. subalpina* from which they are distinct in having slender marginal teeth spread to the ventral lobe bases.

14. *Scapania hollandiae* Hong, Bryologist 83: 56. 1980 E

Plants 4--25 x 1.8--4.5 mm, green to slightly brownish. **Leaves** dentate distally to entire, terminal tooth cell to 1.5 times as long as wide; dorsal lobe 0.55--0.75 times the size of ventral, 1.1--1.4 times as wide as long, arcuately inserted, crossing stem, divergent with it, broadly rounded at apex; ventral lobe (0.65--0.75--0.95(--1.1) times as wide as long, arcuately inserted, broadly rounded at apex, not hyaline near base margin; keel 0.25--0.5 times the length of ventral lobe, acute, indistinctly arched, wing narrow to rather broad, entire. **Median leaf cells** with small acute trigones; marginal cells smaller than median, more or less thick-walled, (10--12--15(--17) μm where subisodiametric; oil bodies not persistent; cuticle slightly to moderately papillose. **Specialized asexual reproduction** by gemmae unknown. **Sexual condition** dioicous. **Perianth** strongly compressed, mouth dentate.

Silt over rocks, peaty soil and rotten wood; 700--2500 m; B.C.; Wash., Wyo.

In leaf shape, insertion and dentition as well as in size of plants *S. hollandiae* is most close to robust phases of *S. brevicaulis* often recorded as *S. degenii*. It differs from them in its inability to produce gemmae and deep brown pigmentation, thick-walled marginal cells, and not persistent oil bodies.

15. *Scapania spitsbergensis* (Lindberg) K. Müller (Freiburg), Bull. Herb. Boissier (ser.2) 1: 607. 1901 “spitzbergensis”

Martinellius spitsbergensis Lindberg, Kongl. Svenska Vet.-Akad. Handl.23(5): 31. 1889;
Scapania convexula K. Müller (Freiburg)

Plants 10--75 x 1.5--3.5 mm, green to brown and purplish. **Leaves** dentate-ciliate basally, terminal tooth cell 2--3 times as long as wide; dorsal lobe 0.5--0.75 times the size of ventral, 1.0--1.35 times as wide as long, decurrent, extending beyond stem, divergent with it, rounded to obscurely pointed at apex; ventral lobe 0.85--1.15 times as wide as long, decurrent proximal to keel insertion, rounded to obscurely pointed at apex, not hyaline near base margin; keel 0.1--0.35 times the length of ventral lobe, acute, moderately to strongly arched, wing mostly broad, dentate. **Median leaf cells** with small acute to large bulging trigones; marginal cells usually thick-walled, 16--18 μm where subisodiametric; oil bodies not persistent; cuticle slightly to coarsely papillose. **Specialized asexual reproduction** by gemmae sporadic, green to purplish and brownish in sun, 2-celled, ovoid, ellipsoid, 11--19 x 23--34(--38) μm . **Sexual condition** monoicous (paroicous). **Perianth** strongly compressed, mouth dentate to lobulate-ciliate.

Soil and rocks in Arctic and in mountains southward; 0--1600 m; Greenland; B.C., N.W.T., Ont., Yukon; Alaska, Maine; Europe (Finland, Norway, Russia, Svalbard, Sweden); Asia (Russia).

Scapania spitsbergensis, on account of its frequently dentate keel, may be confused with *S. undulata* var. *oakesii* and some phases of *S. nemorea*. From both it is distinct in monoicous sexuality and in marginal teeth developed primarily near leaf bases. Male bracts that are proximal to the perianth in *S. spitsbergensis*, however, do not differ from sterile leaves, and the detection of antheridia in the bract axils is necessary for determining sexuality. Distinction from *S. undulata* is by the more narrow terminal tooth cells and frequent development of moderate often bulging trigones. An additional character distinguishing *S. nemorea* from *S. spitsbergensis* is the common production of 1-celled brown gemmae (vs. 2-celled green to pinkish gemmae).

16. *Scapania subalpina* (Nees ex Lindenber) Dumortier, Recueil Observ. Jungerm., 14. 1835

Jungermannia subalpina Nees ex Lindenber, Syn. Hep. Eur. 55.1829; *Scapania perlaxa* Warnstorf

Plants 10--50 x 1.5--4 mm, whitish green to reddish brown. **Leaves** denticulate distally to subentire, terminal tooth cell to 1.5 times as long as wide; dorsal lobe 0.65--0.8 times the size of ventral, 0.85--1.4 times as wide as long, subtransversely inserted, mostly extending to far edge of stem or slightly beyond it, divergent with stem, broadly rounded to weakly pointed at apex; ventral lobe 0.8--1.1 times as wide as long, decurrent proximal to keel insertion, broadly rounded to weakly pointed at apex, not hyaline near base margin; keel (0.4--0.5--0.65) times the length of ventral lobe, acute, indistinctly arched, wing mostly narrow, entire. **Median leaf cells** with small acute trigones; marginal cells mostly thick-walled, 16--22 μm where subisodiametric; oil bodies not persistent; cuticle smooth to slightly papillose. **Specialized asexual reproduction** by gemmae sporadic, green to reddish, 2-celled, broadly ovoid, 12--19 x 19--28 μm . **Sexual condition** dioicous. **Perianth** strongly compressed, mouth dentate.

Mostly on moist rocks in or near moving water, more rarely on moist soil and rotten wood, from Arctic to high altitudes southward; 200--3800 m; Greenland; Alta., B.C., Man., Nfld., N.W.T., N.S., Ont., Que., Sask., Yukon; Alaska, Ariz., Calif., Colo., Kans., Maine, Mich., Minn., Mont., Nebr., Nev., N.H., N.Mex., N.Y., N.Dak., Oreg., S.Dak., Tex., Utah, Wash., Wis., Wyo.; Eurasia; Atlantic Islands.

The elevational range of *Scapania subalpina* is incompletely known. *Scapania subalpina* may be confused with *S. undulata* and *S. obscura* considered above. It differs from the former in its larger dorsal lobe, usually whitish green (vs. grass-green) color of unpigmented forms and reddish brown (vs. vinaceous or purplish violet) color of pigmented forms. Small forms may be confused with *S. curta*. They are distinct in that the ventral lobe of *S. subalpina* is decurrent proximal to the keel insertion. A minor variant is *Scapania subalpina* var. *muddiae* C. D. Bird & W. S. Hong, known only from Alberta. It is distinguished by almost entire leaf margins and a larger perianth (4--8 x 1.5--2 mm).

17. *Scapania obscura* (Arnell & Jensen) Schiffner, Oesterr. Bot. Z. 58: 377. 1908

Martinellius obscurus Arnell & Jensen, Naturwiss. Untersuch. Sarekgebirges Schwed.-Lappl., Bot. 91. 1907

Plants 3--20 x 1--2(--3) mm, green to fuscous or blackish. **Leaves** entire; dorsal lobe 0.65--0.8 times the size of ventral, 0.6--1.27 times as wide as long, subtransversely inserted or decurrent, mostly extending to far edge of stem or slightly beyond it, divergent with stem, rounded to bluntly pointed at apex; ventral lobe 0.4--1.0 times as wide as long, decurrent proximal to keel insertion, rounded to bluntly pointed at apex, not hyaline near base margin; keel 0.5--0.75 times the length of ventral lobe, rounded to acute, indistinctly to moderately arched, wing absent. **Median leaf cells** with very minute to small acute trigones; marginal cells mostly not differentiated, 16--23 μ m where subisodiametric; oil bodies not persistent; cuticle slightly papillose. **Specialized asexual reproduction** by gemmae sporadic, green to brown and purple, 1--2-celled, broadly ovoid, 7--14 x 12--21(--26) μ m. **Sexual condition** dioicous. **Perianth** compressed, mouth entire.

Confined to melt-water rivulets, brooks, springs, and seepages, upper subalpine and alpine zones, rarely in damp tundras; 200--2000 m; Greenland; B.C., N.W.T., Nunavut; Alaska, Ore., Wash.; Eurasia.

T. C. Frye and L. Clark (1937--1947) described *S. subalpina* var. *haynesiae* from Alberta. According to the original description it corresponds more to *S. obscura* than to *S. subalpina* in having leaves not bordered and entire; the keels that are 1 cell thick and rounded throughout their length; and the cortex differentiated by the color rather than by thickness of the cell walls. The reddish brown pigmentation of the plants, however, usually does not occur in *S. obscura* and is characteristic for *S. subalpina*. This makes the exact position of this variety ambiguous until revision of the original collections, which were unavailable for study. *Scapania obscura* is usually distinct from *S. subalpina* in the leaves being entire and not bordered with a weakly defined keel; cortex, defined by pigmentation mostly; fuscous (vs. reddish brown) pigmentation

of plants; and 1--2-celled gemmae. The leaves of *S. obscura* are occasionally upturned. Impoverished plants of *S. obscura* illustrated by A. D. Potemkin (1998: Figs. 3: 1, 3--5) may be misidentified as species of *Lophozia* s. l. They are distinct from the latter in broadly ovoid gemmae, often conduplicate upper leaves and cells nearly without trigones.

18. *Scapania undulata* (Linneaus) Dumortier, Recueil Observ. Jungerm. 14. 1835

Jungermannia undulata Linneaus, Spec. Pl. (ed.1) 2: 1132. 1753

Plants 15--200 x 1.5--4.5 mm, green to brown and purple at least postically. **Leaves** dentate predominantly distally to entire, terminal tooth cell to 1.5 times as long as wide; dorsal lobe 0.35--0.65 times the size of ventral, (0.6--0.95--1.3 times as wide as long, subtransversely inserted, mostly extending to far edge of stem or slightly beyond it, divergent with stem, broadly rounded to weakly pointed at apex; ventral lobe 0.7--1 times as wide as long, decurrent proximal to keel insertion, broadly rounded to weakly pointed at apex, not hyaline near base margin; keel 0.25--0.5 times the length of ventral lobe, acute, indistinctly to moderately arched, wing narrow to broad, occasionally dentate. **Median leaf cells** with minute to moderate acute trigones; marginal cells thick-walled and small, 12--16 μm (terrestrial forms) to thin-walled and larger (aquatic forms), 16--20 μm where subisodiametric; oil bodies not persistent; cuticle smooth. **Specialized asexual reproduction** by gemmae sporadic, green to purplish in sun, 2-celled, broadly ovoid, 10--17 x 12--23 μm . **Sexual condition** dioicous. **Perianth** strongly compressed, mouth dentate to entire.

Hydric to nearly xeric sites; mostly associated with moving water and rocks; 0--3300 m; Greenland; St. Pierre and Miquelon; Alta., B.C., Man., N.B., Nfld., N.W.T., N.S., Ont., P.E.I., Que., Sask., Yukon; Alaska, Ariz., Ark., Calif., Colo., Conn., Ga., Idaho, Kans., Ky., Maine, Mass., Mich., Minn., Miss., Mo., Mont., Nebr., Nev., N.H., N.J., N.Mex., N.Y., N.C., N.Dak., Ohio, Oreg., Pa., R. I., S. C., S.Dak., Tenn., Tex., Utah, Vt., Va., Wash., W. Va., Wis., Wyo.; Mexico?; Eurasia; n Africa; Atlantic Islands.

Scapania undulata is most often confused with *S. subalpina* considered above and with eastern North American *S. nemorea* subsp. *nemorea*. It is distinct from the latter in slightly elongated terminal tooth cells (mostly not over 1.5 times as long as wide); non-decurrent dorsal lobes; broadly ovoid, green to purplish 2-celled gemmae; predominantly not flattened cortical cells; small oil bodies, occluding considerably less than half of cell lumen (vs. more or less large oil bodies, occluding mostly half or more cell lumen). A minor variant is *Scapania undulata* var. *oakesii* (Austin) H. Buch, of scattered distribution. It is distinguished by the keel often bearing teeth and the dorsal lobe extended across and beyond the stem. Another minor variant known only from Greenland and Europe is *Scapania undulata* var. *aequatiformis* De Notaris. It differs in the suborbicular, broader ventral and dorsal lobes, the keel short and weakly arched.

19. *Scapania serrulata* R. M. Schuster, Hep. Anth. N. Am. 3: 539. 1974 E

Plants 10--25 x 1.8--3.1 mm, green to red and brown. **Leaves** dentate distally, terminal tooth cell to 1.5 times as long as wide; dorsal lobe 0.65--0.75 times the size of ventral, 0.95--1.15 times as wide as long, subtransversely to arcuately inserted, extending to far edge of stem or slightly

beyond it, divergent with stem, broadly rounded at apex; ventral lobe 0.74--0.91 times as wide as long, decurrent proximal to keel insertion, broadly rounded at apex, not hyaline near base margin; keel 0.45--0.65 times the length of ventral lobe, acute, indistinctly to moderately arched, wing narrow to broad, entire to crispate. **Median leaf cells** with moderate bulging to acute trigones; marginal cells mostly thin-walled, often elongated, 20--26(--28) μm where subisodiametric; oil bodies not persistent; cuticle smooth. **Specialized asexual reproduction** by gemmae apparently frequent, green to red, 1--2-celled, broadly ovoid, 16--24 x 22--39 μm . **Sexual condition** dioicous. **Perianth** unknown.

Seepage-moistened soil between rocks, in turbulent streams from snow and ice fields in the Arctic; 200--1000 m; Greenland; N.W.T.

20. *Scapania uliginosa* (Lindenberg) Dumortier, Recueil Observ. Jungerm. 14. 1835

Jungermannia undulata var. *uliginosa* Lindenberg, Syn. Hep. Eur. 58. 1829; *Scapania paludosa* (Müll. Frib.) Müll. Frib.

Plants 20--200 x 1.5--6 mm, green to purple and brown. **Leaves** entire to dentate distally; terminal tooth cell to 1.8 times as long as wide; dorsal lobe 0.25--0.65(--0.8) times the size of ventral, 0.9--1.55 times as wide as long, decurrent, extending far beyond stem, subparallel it, rounded to obtusely pointed at apex; ventral lobe 0.8--1.45 times as wide as long, decurrent proximal to keel insertion, rounded at apex, not hyaline near base margin; keel (0.05--)0.15--0.35 times the length of ventral lobe, acute, moderately to strongly arched, wing narrow to broad, entire. **Median leaf cells** with small to moderate acute trigones; marginal cells thin-walled (entire-leaved forms) to more or less thick-walled (dentate-leaved forms), 15--21 μm where subisodiametric; oil bodies not persistent; cuticle smooth to densely punctate papillose. **Specialized asexual reproduction** by gemmae very rare, green to red, 1-celled, ellipsoid, 8--10 x 13--19 μm . **Sexual condition** dioicous. **Perianth** strongly compressed, mouth entire to denticulate.

Stones in streams and seepage-moistened rocks in mountains and the Arctic, high elevations southward; 200--3800 m; Greenland; Alta., B.C., Nfld., N.W.T., Que., Yukon; Alaska, Colo., Idaho, Maine, Mont., N.H., Oreg., Vt., Wash.; Eurasia.

The elevational range of *Scapania uliginosa* is incompletely known. Forms of *S. uliginosa* with thin-walled marginal cells may be confused with *S. paludicola* from which they are distinct in the ventral lobes being broadly decurrent proximal to the keel insertion and mostly strongly turned backward, and in the usual absence of trigones in leaf cells. The synonymy of *S. uliginosa* and *S. paludosa* is accepted, following D. R. Zehr (1980), because of the minor taxonomic significance of characters ascribed to both names and their frequent occurrence in diverse combinations (A. D. Potemkin 1999a). Forms with dentate and bordered leaves (*S. paludosa*-phases) may be confused with *S. undulata* and *S. spitsbergensis*. They are distinct from the former in the dorsal lobes decurrent and subparallel to the stem and from the latter in marginal teeth not spread to leaf bases and to keel, slightly elongated terminal tooth cells and dioicous sexuality. Sporadic development of leaves with very short keels (to 0.05 times the length of the

ventral lobe) may lead to confusion with *S. ornithopoides* from which *S. uliginosa* differs in marginal teeth not spreading to leaf bases and with slightly elongated terminal cells, inability to produce large trigones, and frequent development of purple pigmentation in the distal portion of leaves.

21. *Scapania cuspiduligera* (Nees) K. Müller (Freiburg), Rabenhorst, Krypogamenfl. Deutschlands (ed.2) 6(2): 472. 1915

Jungermannia cuspiduligera Nees, Naturges. Eur. Leberm.1: 180.1833

Plants 5--20 x 1--2.5 mm, green to fuscous. **Leaves** entire to faintly denticulate distally; dorsal lobe 0.5--0.9 times the size of ventral, 0.5--0.85 times as wide as long, subtransversely inserted, not extending to far edge of stem, divergent with it, rounded to mucronate at apex; ventral lobe 0.5--0.85 times as wide as long, decurrent proximal to keel insertion, rounded to mucronate at apex, hyaline near base margin; keel 0.6--0.75 times the length of ventral lobe, rounded and subparallel to stem basally, more or less acute and divergent with stem distally, wing absent. **Median leaf cells** with small to moderate trigones; marginal cells thick-walled, 15--20 μm where subisodiametric; oil bodies not persistent; cuticle smooth to moderately papillose. **Specialized asexual reproduction** by gemmae, common, brown at least in sun, 2-celled, broadly ovoid, 10--16 x 14--25 μm . **Sexual condition** dioicous. **Perianth** compressed, mouth entire to faintly denticulate.

Varieties 2 (2 in the flora): Greenland, Canada, United States, South America, Eurasia, Africa.

Scapania cuspiduligera is distinct from the other *Scapania* species in the following character states: keel rounded and subparallel to the stem basally and spread out only distally; sheathing leaf bases; rather long decurrent and hyaline ventral lobe base; constant production of brown, 2-celled gemmae with deeper pigmented internal walls; subequal bordered entire leaf lobes with broadly rounded apices.

1. Ventral leaf lobes not falcate, gemmiparous lobes entire; gemmae brown . . . 21a. *Scapania cuspiduligera* var. *cuspiduligera*

1. Ventral leaf lobes falcate, gemmiparous lobes occasionally denticulate; gemmae green becoming brown when mature . . . 21b. *Scapania cupiduligera* var. *diplophyllopsis*

21a. *Scapania cuspiduligera* (Nees) K. Müller (Freiburg) var. **cuspiduligera**

Ventral leaf lobes not falcate, gemmiparous lobes entire. **Gemmae** brown.

Mostly calcareous soils and rocks from the high Arctic to New Mexico, southward at high elevations; 0--3100 m; Greenland; Alta., B.C., Man., N.B., Nfld., N.W.T., N.S., Ont., Que., Sask., Yukon; Alaska, Ariz., Calif., Colo., Idaho, Mich., Minn., Mont., Nev., N.Mex., Oreg., Utah, Vt., Wash., Wis., Wyo.; South America (Colombia), Eurasia; Africa (Republic of the Congo).

The gemmae of *Scapania cuspiduligera* var. *cuspidula* are brown, 2-celled, and have deeply pigmented internal cell walls.

21b. *Scapania cuspiduligera* var. *diplophylopsis* R. M. Schuster, Hepat. Anthocerotae N. Amer. 3: 361. fig. 371: 1--14. 1974

Ventral leaf lobes falcate, gemmiparous lobes occasionally denticulate. **Gemmae** green but becoming brown when mature.

Habitat not given; low to moderate elevations; Greenland.

22. *Scapania hians* Stephani ex K. Müller (Freiburg), Nova Acta Acad. Caes. Leop. -Carol. German. Nat. Cur.83: 223. 1905

Subspecies 2 (1 in the flora): Canada; Asia (China, India (Sikkim: reported by T. Herzog (1939) as *S. papillosa* K. Müller (Freiburg)), Nepal).

22a. *Scapania hians* subsp. *salishensis* J. Godfrey & G. Godfrey, Bryologist 81: 362. 1978

Plants 5--22 x 0.85--1.6 mm, brownish green. **Leaves** entire to slightly denticulate distally; dorsal lobe 0.75--0.95 times the size of ventral, 0.55--0.7 times as wide as long, more or less arcuately inserted, crossing stem, divergent with it, triangular and pointed at apex; ventral lobe 0.5--0.65(--0.8) times as wide as long, decurrent proximal to keel insertion, triangular and pointed at apex, not hyaline near base margin; keel 0.4--0.7 times the length of ventral lobe, acute, indistinctly to moderately arched, wing mostly absent. **Median leaf cells** with more or less small acute to slightly bulging trigones; marginal cells smaller than median, thin- to slightly thick-walled, 10--14 μm where subsodiametric; oil bodies not persistent; cuticle coarsely papillose. **Specialized asexual reproduction** by gemmae, frequent, brown, (1--)2-celled, spherical to ovoid, 10--16 x 10--20(--24) μm . **Sexual condition:** perianth and sex organs unknown.

Silt over rocks, wet or submerged in glacier-fed mountain streams, forest to subalpine belts; of conservation concern; 500--1400 m; B.C.

Scapania hians is distinct from the other *Scapania* in its marsupelloid appearance with the ventral lobe decurrent proximal to the keel insertion and brown gemmae at shoot apices. It also differs from the similar *S. aequiloba* in its long-decurrent (vs. short-decurrent) ventral lobe, brown (vs. green) gemmae, and weaker development of marginal denticulation and border. The subsp. *salishensis* has lobes mostly stiffly spreading from each other.

23. *Scapania mucronata* Buch, Meddeland Soc. Fauna Fl. Fenn. 42: 91. 1916

Plants 3--12 x 0.7--2.8(--3) mm, green to brown. **Leaves** entire or remotely denticulate distally; dorsal lobe 0.45--0.75(--0.85) times the size of ventral, 0.6--0.85 times as wide as long, subtransversely inserted, not extending to far edge of stem, divergent with it, mucronate to apiculate at apex; ventral lobe 0.4--0.8 times as wide as long, subtransversely inserted, obtuse to

mucronate at apex, not hyaline near base margin; keel 0.5--0.75 times the length of ventral lobe, rounded to acute, indistinctly to moderately arched, wing absent. **Median leaf cells** with moderate, acute to bulging trigones; marginal cells not differentiated, 14--20 μm where subisodiametric; oil bodies not persistent; cuticle slightly to moderately papillose. **Specialized asexual reproduction** by gemmae, common, green, reddish or brownish in sun, 2-celled, ovoid, 10--19 x 18--36 μm . **Sexual condition** dioicous. **Perianth** slightly compressed, mouth lobulate-dentate.

Subspecies 2 (2 in the flora): Northern Hemisphere.

1. Dorsal lobe 0.45--0.55 times the size of ventral; keel 0.5 times the length of ventral lobe; leaves entire; gemmae green to rarely weakly reddish, 10--14 x 20--25(--29) μm1a. *Scapania mucronata* subsp. *mucronata*

1. Dorsal lobe 0.65--0.85 times the size of ventral; keel 0.6--0.85 times the length of ventral lobe; leaves with occasional 1-celled teeth distally; gemmae green to reddish and brownish, 10--19 x 18--36 μm1b. *Scapania mucronata* subsp. *praetervisiva*

23a. *Scapania mucronata* Buch subsp. *mucronata*

Leaves normally entire; dorsal lobe 0.45--0.55 times the size of ventral; keel 0.5 times the length of ventral lobe, acute. **Specialized asexual reproduction** by gemmae, green to rarely weakly reddish, 10--14 x 20--25(--29) μm .

Rocks and decaying wood, occasionally on soil; 0--3000 m; Greenland; Alta., B.C., Man., N.B., Nfld., N.W.T., N.S., Ont., P.E.I., Que., Sask., Yukon; Ala., Alaska, Ariz., Ark., Calif., Colo., Conn., Del., D.C., Fla., Ga., Idaho, Ill., Ind., Iowa, Kans., Ky., La., Maine, Md., Mass., Mich., Minn., Miss., Mo., Mont., Nebr., Nev., N.H., N.J., N.Mex., N.Y., N.C., N.Dak., Ohio, Oreg., Vt., Va., Wash., Wis., Wyo.; Eurasia; Atlantic Islands.

Scapania mucronata subsp. *mucronata* may be confused with *S. scandica*. It differs from the latter in having the dorsal lobe divergent with the stem, thin-walled marginal cells, invariable absence of purple pigmentation, and a lobulate-dentate perianth mouth. The oil bodies are 2--5 per cell.

23b. *Scapania mucronata* subsp. *praetervisiva* (Meylan) Schuster, Hep. Anth. N. A. 3: 437. 1974

Scapania praetervisiva Meylan, Janresber. Naturf. Ges. Graubündes (ser.2) 64: 364. 1926

Leaves with occasional 1-celled teeth distally; dorsal lobe 0.65--0.75 times the size of ventral; keel 0.6--0.75 times the length of ventral lobe, acute to rounded basally. **Specialized asexual reproduction** by gemmae, green to reddish and brownish, 10--19 x 18--36 μm .

Limy soil and rocks; 0--3700 m; Greenland; B.C., N.W.T.; Alaska, Colo., Idaho, Oreg.; Eurasia.

There are no records of *Scapania mucronata* subsp. *praetervisa* for Yukon and Washington although the subspecies should be expected to occur there. Differentiation of *S. mucronata* subsp. *praetervisa* and *S. zemliae* is considered under the latter species. Similar to subsp. *praetervista* is *S. mucronata* var. *polaris* R; M. Schuster, known from Ellesmere Island of Nunavut. It differs largely in tendency of gemmae to become yellowish to yellowish brown, and the shoots not developing strong secondary pigmentation in sun-lit sites.

24. *Scapania helvetica Gottsche, S. M. Gottsche and L. Rabenhorst, Hep. Eur. [Exsicc.] n. 426.1868

Plants 9--20 x 1.8--2.4 mm, green to brown. **Leaves** entire or with few distal teeth associated with gemma formation; dorsal lobe 0.5--0.65 times the size of ventral, 0.75--0.87 times as wide as long, subtransversely inserted, not extending to far edge of stem, divergent with it, blunt to rounded at apex; ventral lobe 0.75--0.85 times as wide as long, subtransversely inserted, more or less rounded at apex, not hyaline near base margin; keel 0.45--0.6 times the length of ventral lobe, acute, indistinctly to moderately arched, wing absent. **Median leaf cells** with moderate acute, rarely bulging trigones; marginal cells not differentiated, 15--19 μm where subisodiametric; oil bodies not persistent; cuticle slightly to moderately papillose. **Specialized asexual reproduction** by gemmae sporadic, green, 2-celled, ovoid, 10--13 x 16--25 μm . **Sexual condition** dioicous. **Perianth** slightly compressed, mouth shortly dentate to subentire.

Habitat and elevation unknown; Greenland; B.C; Europe.

Habitats, elevation, and distribution of *Scapania helvetica* in the range of the flora remain unclear. Materials of the species from the territory of the flora were unavailable for study and this remains to be the only reason to include the species description in the flora. The record of the species from Greenland (H. W. Arnell 1922) is far outside its European range and may be based on impoverished plants of *S. hyperborea*. The report of *S. helvetica* from British Columbia is also very doubtful (R. M. Schuster 1974: 457). In Europe *S. helvetica* occurs on soil and rocks in alpine and subalpine areas; and as mentioned by K. Müller (1951--1958) at elevations to 1850 m. *Scapania helvetica* is distinct from the other species of the sect. *Curtae* in having mature leaves with blunt to rounded dorsal lobe apices. It may be distinguished from small phases of *S. hyperborea* by green ovoid (vs. often purple to brown, broadly ovoid) gemmae.

25. Scapania zemliae Arnell, Svensk Bot. Tidskr.41(2): 215. 1947

Scapania invisita Schuster

Plants 2--15 mm x 0.5--2 mm, green to brown. **Leaves** entire to denticulate distally; dorsal lobe 0.3--0.65 ventral, 0.69--0.83 times as wide as long, subtransversely inserted, not extending to distal edge of stem, divergent with it, triangular and sharp-pointed to mucronate at apex; ventral lobe, 0.7--0.8 times as wide as long, subtransversely to arcuately inserted, sharp-pointed to mucronate at apex, not hyaline near base margin; keel 0.45--0.75 times the length of ventral lobe, rounded basally to acute distally, moderately arched, wing mostly absent. **Median leaf cells** with small acute to moderately bulging trigones; marginal cells distinctly smaller than median, occasionally thick-walled, 14--25 μm where subisodiametric; oil bodies not persistent;

cuticle moderately papillose. **Specialized asexual reproduction** by gemmae, common, green to reddish and brown in sun, 2-celled, broadly ovoid to ellipsoid and rhomboid, (11--14--18 x (15--20--35) μm . **Sexual condition** dioicous. **Perianth** moderately compressed, mouth dentate.

An Arctic species, on soil over basaltic rocks and in lava crevices, 0--200 m; Greenland; Alaska; Eurasia (Russian Arctic from Novaya Zemlya to Chukotka, also in mountains of Yakutia in East Siberia,).

Scapania zemliae may be confused with *Scapania mucronata* subsp. *praetervisa* from which it differs in the bordered and upturned leaves, and more numerous (4--10 vs. 3--6) oil bodies in leaf cells. The leaves are upturned.

26. *Scapania lingulata* Buch, Meddeland Soc. Fauna Fl. Fenn.42: 92. 1916

Scapania microphylla Warnstorf, *S. lingulata* var. *microphylla* (Warnstorf) R. M. Schuster

Plants 3--10(--20) x 1--2.5(--3) mm, green to brown, occasionally purple postically. **Leaves** denticulate to irregularly coarsely dentate distally, rarely entire, terminal tooth cell mostly not over x 1.8 as long as wide; dorsal lobe 0.4--0.75(--0.85) ventral, 0.5--0.9 times as wide as long, subtransversely inserted not extending to distal edge of stem, divergent with it, more or less triangular pointed into an apiculate to mucronate apex (apex exceptionally rounded to blunt); ventral lobe more or less lingulate, x 0.45--0.8 times as wide as long, subtransversely to arcuately inserted, rounded to triangular and pointed at apex, not hyaline near base margin; keel 0.4--0.55(--0.7) times the length of ventral lobe, acute, indistinctly to moderately arched, wing occasionally narrow, entire. **Median leaf cells** with moderate, acute to bulging trigones; marginal cells thin- to more or less thick-walled, 18--28 μm where subisodiametric; oil bodies not persistent; cuticle moderately papillose to smooth. **Specialized asexual reproduction** by gemmae, frequent, green to reddish and brownish, (1--2)-celled, narrowly elliptic to broadly ovoid and obtusely angulate, 9--20 x 17--32(--38) μm . **Sexual condition** dioicous. **Perianth** more or less compressed, mouth lobulate-dentate to occasionally sinuate with solitary remote short teeth.

Acid cliffs, ledges, soil, and rotten wood ; 0--2800 m; Greenland; Ont., P.E.I.; Maine, Mass., Mich., Minn., Nevada, Vt., Wis.; Europe, Caucasus, Far East of Russia.

The considerable variability of *Scapania lingulata* in leaf shape, marginal border expression and perianth compression provides a basis for its confusion with other species with parallel variability ranges. It is distinct from *S. curta* in having often coarser leaf dentition, smaller dorsal lobe, gemmae that are variable in shape and, if there is dentate perianth mouth, in mostly spinous terminal tooth cells of the mouth about 2 times as long as wide (vs. more or less obtuse shorter cells); from the regional *S. scandica* in having larger cells with more numerous (6--12 vs. 2--5) oil bodies, divergent with stem dorsal lobe and with marginal cells hardly differentiated in size; from *S. mucronata* in having larger cells, more numerous (6--12 vs. 2--5) oil bodies, often coarsely dentate leaves and sporadic purple pigmentation of ventral lobe bases. Phases with moderately inflated perianths and gemmae, which are green to brownish in the sun (found in Nevada) may be confused with *S. pseudocalcicola* because of the similarity in leaf shape and the variability of the marginal border pattern. They are distinct from the latter in the absence of a

hyaline area near the ventral lobe base; not persistent, smaller (5--7 x 6--9 μm vs. 7--11 x 8--16 μm) and more numerous (6--13 vs. 2--4) oil bodies; often coarsely dentate leaves and in acidophylous ecological requirements (A. D. Potemkin 1999b).

27. *Scapania curta* (Martius) Dumortier, Recueil Observ. Jungerm. 14. 1835

Jungermannia curta Martius, Fl. Crypt. Erlang. 148. 1817; *Scapania curta* var. *grandiretis* R. M. Schuster; *Scapania perssonii* Schuster

Plants 3--15 x 1--2.5(--3) mm, green to brown and purple, especially postically. **Leaves** entire to denticulate distally; dorsal lobe 0.5--0.85 times the size of ventral, 0.5--1.0 times as wide as long, subtransversely inserted, not extending to far edge of stem, divergent with it, rounded at the blunt to mucronate apex; ventral lobe 0.6--0.85(--0.95) times as wide as long, subtransversely inserted, broadly rounded to obtusely pointed at apex, not hyaline near base margin; keel 0.45--0.7 times the length of ventral, acute to more or less rounded, indistinctly to moderately arched, wing absent or narrow, entire. **Median leaf cells** with mostly small to moderate acute trigones; marginal cells hardly differentiated in size, thick- to thin-walled, 18--28 μm where subisodiametric; oil bodies not persistent; cuticle smooth to slightly papillose. **Specialized asexual reproduction** by gemmae, sporadic, green, 2-celled, more or less narrowly ovoid, 11--20 x 18--38 μm . **Sexual condition** dioicous. **Perianth** more or less compressed, mouth subentire to dentate.

Bare acid to neutral soil and rocks, or weakly covered by bryophytes, from Arctic to uplands southward; 0--3700 m; Greenland; Alta., B.C., Man., Nfld., N.W.T., Nunavut, N.S., Ont., P.E.I., Que., Sask., Yukon; Alaska, Ariz., Calif., Colo., Idaho, Kans., Maine, Mich., Minn., Mont., Nebr., Nev., N.H., N.Mex., N.Y., N.Dak., Oreg., S.Dak., Tex., Utah, Wash., Wis., Wyo.; Eurasia; Africa (Mediterranean area); Atlantic Islands.

There are no records of *Scapania curta* for St. Pierre and Miquelon and N.B. although the species should be expected to occur there. Plants of *S. curta* without marginal borders of thick-walled cells may be confused with *S. obcordata*. They differ from the latter species in the leaves being sporadically denticulate distally with locally thick-walled marginal cells devoid of oil bodies and gemmae, which are more narrow, green or hardly reddish, when in sun. *Scapania perssonii* is considered as a large-celled phase of *S. curta* with or without a weakly defined marginal border. It corresponds to *S. curta* var. *grandiretis* Schuster (A. D. Potemkin 1999a). This large-celled variety may be confused with *S. lingulata*, from which it is distinct in its larger dorsal lobe, inability to develop coarse leaf dentition, rather uniform in gemma shape, and subentire to slightly dentate perianth mouth with obtuse terminal tooth cells. The leaves are occasionally upturned. A minor variant known only from Greenland, *Scapania curta* var. *isoloba* R. M. Schuster, differs in marginal cells small, 18--20 μm and dorsal lobe 0.75--0.85 the size of the ventral lobe.

28. *Scapania obcordata* (Berggren) Arnell, Ark. Bot. (ser.2) 4(6): 117. 1959

Sarcoscyphus obcordatus Berggren, Kongl. Svenska Vetensk.-Akad. Handl.13: 96. 1875;
Scapania paradoxa R. M. Schuster

Plants 3--18 x 0.8--2.8 mm, green to brown and purple. **Leaves** entire; dorsal lobe 0.55--0.95 times the size of ventral, 0.6--0.7 times as wide as long, subtransversely inserted, not extending to distal edge of stem, divergent with it, obtuse to triangular and narrowed to sharp apex; ventral lobe 0.72--0.95 times as wide as long, subtransversely inserted, obtuse to broadly rounded at apex, not hyaline near base margin; keel 0.37--0.75 times the length of ventral lobe, rounded at least basally, indistinctly arched, wing absent. **Median leaf cells** with small acute trigones; marginal cells usually not differentiated, 12--29 μm where subisodiametric; oil bodies not persistent; cuticle smooth to slightly papillose. **Specialized asexual reproduction** by gemmae, frequent, green to purple, (1--)2-celled, broadly ovoid, 12--24 x 14--36 μm . **Sexual condition** dioicous. **Perianth** more or less inflated, mouth entire to shallowly lobulate-dentate.

Tundra communities on mostly neutral to acid soils, late snow areas, and banks of water courses in Arctic and Subarctic territories; 0--1400 m; Greenland; N.W.T., Que.; Alaska; Eurasia (n Finland, Iceland, Norway, Russia, Svalbard, n Sweden).

There are no records of *Scapania obcordata* for Yukon although the species should be expected to occur there. *S. obcordata* is an exceedingly malleable Arctic species, producing diverse forms from lophozoid to typical scapanioid. Important distinctive characters of the species are entire emarginate leaves, invariably small acute trigones, broadly ovoid gemmae, and frequent (but not constant) development of purple pigmentation. Some populations of the species are characterized by the common development of *Radula*-type terminal branching, occurring rarely in the other species of *Scapania*. *Scapania paradoxa* is considered as a synonym of *S. obcordata* after A. D. Potemkin (1998b). The leaves are often upturned. *Scapania paradoxa* var. *ramose* R. M. Schuster, known only from Greenland, is smaller in several respects and branches abundantly.

29. *Scapania scandica* (Arnell & H. Buch) Macvicar, Stud. Hand. Brit. Hep. (ed. 2): 394. 1926

Martinellius scandicus Arnell & H. Buch, Bot. Not. 1921: 1. 1921; *Scapania parvifolia* Warnstorf

Plants 5--20 x 1--2.5 mm, green to brown and purple, especially postically. **Leaves** dentate distally, teeth 1--3 cells long, terminal tooth cell mostly to 1.5 times as long as wide; dorsal lobe 0.35--0.65 times the size of ventral, 0.6--0.85(--1) times as wide as long, subtransversely inserted, not extending to distal edge of stem, subparallel to it, mucronate at apex; ventral lobe 0.45--0.75 times as wide as long, subtransversely inserted, rounded to triangular and pointed at apex, not hyaline near base margin; keel 0.25--0.5 times the length of ventral lobe, acute, indistinctly to moderately arched, wing absent. **Median leaf cells** with small acute to moderate bulging trigones; marginal cells strongly to slightly differentiated in size, thin- to thick-walled, 12--20 μm where subisodiametric; oil bodies not persistent; cuticle slightly to moderately papillose. **Specialized asexual reproduction** by gemmae, frequent, green, 2-celled, narrowly ovoid, 7--13 x 18--25 μm . **Sexual condition** dioicous. **Perianth** more or less compressed, mouth entire to dentate-ciliate.

Mostly neutral to acid mineral, humic and peaty soils slightly covered by bryophytes; 0--1500 m; Greenland; B.C., Nfld., N.W.T., N.S., Ont., Que.; Alaska, Maine, Mass, N.Y., Wash., Wis.; Eurasia; Atlantic Islands.

There are no records of *Scapania scandica* for Yukon although the species should be expected to occur there. *Scapania scandica* is distinct from the other species of sect. *Curtae* in its dorsal lobe being mainly subparallel to the stem, free lobe dentition mostly connected with gemma production, and marginal cells strongly differentiated in size when they are thick-walled. The east Asian *Scapania scandica* var. *grandiretis* (Schljakov) Schljakov has been reported from California (Bakalin 2012). A minor variant from one site in Nova Scotia is *Scapania scandica* var. *dimorpha* R. M. Schuster. It differs in gemmiparous leaves smaller, with subequal, ciliate lobes.

SELECTED REFERENCE: Bakalin, V. A. 2012a. A small collection of hepatics from Oregon and California (western North America). *Arctoa* 21: 201–205.

30. *Scapania fulfordiae* W. S. Hong, *Bryologist* 83(1): 46. 1980 E

Plants 3--6 x 0.5--1.2 mm, green to yellowish. **Leaves** entire; dorsal lobe 0.4--0.8 times the size of ventral, 0.6--0.8 times as wide as long, subtransversely inserted, not extending to far edge of stem, divergent with it, blunt to triangular and pointed at apex; ventral lobe 0.5--0.75 times as wide as long, subtransversely inserted, broadly rounded to mucronate at apex, not hyaline near base margin; keel 0.3--0.6(--0.75) times the length of ventral lobe, cross section morphology unknown, indistinctly arched, wing absent. **Median leaf cells** with small acute trigones; marginal cells not differentiated, 10--14 μm where subisodiametric; oil bodies not persistent; cuticle slightly papillose. **Specialized asexual reproduction** by gemmae, common, green, 1-celled, ovoid to narrowly ovoid, 5--8 x 14--20 μm . **Sexual condition** perianth and sex organs unknown.

Wet humus over rocks along snow melt mountain streams in alpine forests; 3500 m; Colo., Wyo.

Material of the species was unavailable for study. This description is based on the original description and illustrations only (W. S. Hong 1980). The position of the species within the genus remains unclear. It is the only American species of *Scapania* with green 1-celled gemmae. *Scapania fulfordiae* should be considered an endemic of North America and a species of conservation concern.

31. *Scapania irrigua* (Nees) Nees, *Syn. Hep.*, 67. 1844

Jungermannia irrigua Nees, *Naturgesch. Eur. Leberm.* 1: 175, 193. 183.

Plants 10--50 x 2--4 mm, green to brown and red. **Leaves** entire to denticulate distally; dorsal lobe 0.5--0.6 times the length of the ventral, 0.65--1 times as wide as long, subtransversely inserted, mostly extending to far edge of stem or slightly beyond it, divergent with stem, obtuse to sharply pointed at apex; ventral lobe (0.75--)0.85--1.05(--1.15) times as wide as long,

arcuately inserted, obtuse to sharply pointed at apex, not hyaline near base margin; keel 0.35--0.5 times the length of ventral lobe, acute, moderately arched, wing mostly absent. **Median leaf cells** with small acute to moderate bulging trigones; marginal cells not differentiated, 16--21 μm where subisodiametric; oil bodies not persistent; cuticle slightly to moderately papillose. **Specialized asexual reproduction** by gemmae sporadic, green, 2-celled, narrowly ovoid, 9--12 x 20--28 μm . **Sexual condition** dioicous. **Perianth** compressed, mouth entire to dentate.

Boggy places, on decaying wet logs and moist soil; 0--3600 m ; Greenland; Alta., B.C., Man., N.B., Nfld., N.W.T., N.S., Ont., P.E.I., Que., Sask., Yukon; Alaska, Ariz., Calif., Colo., Conn., Idaho, Maine, Mich., Minn., Mont., Nebr., Nev., N.H., N.J., N.Mex., N.Y., N.Dak., Oreg., Pa., S.Dak., Tex., Utah, Vt., Wash., Wis., Wyo.; Eurasia; (n Africa); Atlantic Islands (Madeira).

Scapania irrigua is often confused with *S. hyperborea* considered above and with *S. paludicola*. It is distinct from *S. paludicola* in its narrower dorsal lobes which are not decurrent and divergent with the stem and invariably green gemmae. The latter character fails to work only for differentiation of *S. irrigua* and rare *S. paludicola* var. *viridigemma* Schuster. A minor variant reported for Greenland, Quebec and Minnesota is *S. irrigua* subsp. *rufescens* (Loeske) R. M. Schuster. It differs in the combination of leaf lobes rounded to blunt and secondary pigmentation reddish.

32. *Scapania hyperborea* Jørgensen, Fl. Nord.-Reisen: 56. 1894

Plants 10--30 x 1.5--4 mm, green to brown, rarely purplish postically. **Leaves** entire or crooked to dentate mostly distally with small to large broad-based teeth; terminal tooth cell to 1.5 times as long as wide; dorsal lobe 0.5--0.75(--0.8) times the size of ventral, 0.8--1.3 times as wide as long, subtransversely inserted, mostly extending to far edge of stem or slightly beyond it, divergent with stem, rounded to acute at apex; ventral lobe 0.8--1.1(--1.15) times as wide as long, decurrent to keel insertion, rounded to triangular and pointed at apex, not hyaline near base margin; keel (0.2--)0.3--0.5 times the length of ventral lobe, more or less acute, moderately to strongly arched, wing absent or occasionally broad, entire to dentate. **Median leaf cells** with moderate, mostly bulging trigones; marginal cells not differentiated, (14--)16--20 to 23--32 μm where subisodiametric; oil bodies not persistent; cuticle slightly to moderately papillose. **Specialized asexual reproduction** by gemmae sporadic, green to fuscous and deep purple, (1--)2-celled, broadly ovoid, 10--21 x 12--31(--33) μm . **Sexual condition** dioicous. **Perianth** moderately compressed, mouth entire to dentate.

Peaty and sandy moist soil in tundra and alpine communities; 0--3800 m; Greenland; N.W.T., Ont.; Alaska, Colo., Maine, N.H.; Europe (Iceland, Norway, Finland, n Russia, Svalbard, Sweden); Asia (n Russia).

There are no records of *Scapania hyperborea* for Yukon, Quebec, and Newfoundland although the species should be expected to occur there. The Colorado record is doubtful. The extreme variability of *S. hyperborea* has led to its confusion with *S. irrigua*, *S. brevicaulis*, and *S. helvetica*. The most reliable distinctive feature of diverse forms of *S. hyperborea* is the broadly ovoid, easily turning purple or fuscous, mostly 2-celled gemmae vs. narrowly ovoid green gemmae of *S. irrigua* and *S. helvetica* and in most cases largely 1-celled brown gemmae of *S.*

brevicaulis. One-celled gemmae are known for some forms of large-celled *S. tundrae* (K. Müller 1951--1958) considered to be a variety of *S. hyperborea* (*S. hyperborea* var. *tundrae* (Arnell) Potemkin (A. D. Potemkin 1999a). Additional distinction between typical variety of *S. hyperborea* and *S. brevicaulis* are the usually not persistent oil bodies and large bulging trigones. Differentiation of non-gemmiparous plants of the considered species is often very questionable. *S. hyperborea* var. *hyperborea* may be easily confused with plants of *S. brevicaulis* with largely 2-celled gemmae, known as *S. degenii* var. *dubia* Schuster. They are distinct from the latter in having a slightly arched keel usually without a wing, invariably entire leaves, mostly more broad and never citron-shaped, and frequently reddish gemmae. The leaves are sporadically upturned.

Varieties 2 (2 in the flora): their ecological requirements and distribution are similar.

1. Leaf margins smooth, never crooked. Marginal leaf cells (14)16--20 μm 32a. *Scapania hyperborea* var. *hyperborea*
2. Leaf margins more or less crooked to more or less dentate. Marginal leaf cells 23--32 μm 32b. *Scapania hyperborea* var. *tundrae*

32a. *Scapania hyperborea* Jørgensen var. *hyperborea*

Leaf margins smooth, never crooked. **Marginal leaf cells** (14)16--20 μm .

Ecological requirements and distribution are listed above under species description.

32b. *Scapania hyperborea* var. *tundrae* (Arnell) Potemkin
Scapania pulcherrima R. M. Schuster; *S. tundrae* (Arnell) H. Buch

Leaf margins more or less crooked to more or less dentate. **Marginal leaf cells** 23--32 μm .

This variety is distinct from all species in the flora in having large cells (23--32 μm along margins) and often crooked to dentate leaf margins. According to recent molecular studies (J. Heinrichs et al., 2012) *S. hyperborea* var. *tundrae* is distinguished as a separate species, *S. tundrae*.

Ecological requirements and distribution are listed above under species description.

33. *Scapania paludicola* Loeske & K. Müller (Freiburg), Lebermoose 2: 425. 1915

Plants 30--80 x 2.5--4.5 mm, green to brown, occasionally purplish postically. **Leaves** entire to rarely dentate distally, terminal tooth cell 1.3--2 times as long as wide; dorsal lobe 0.5--0.6 times the size of ventral, 1.3--1.5(--2) times as wide as long, decurrent, extending far beyond stem, subparallel to slightly divergent with it, rounded to pointed at apex; ventral lobe 0.85--1.35 times as wide as long, decurrent to about keel insertion, apiculate to rounded at apex, not hyaline near base margin; keel (0.05--)0.15--0.25(--0.3) times the length of ventral lobe, acute, strongly arched, wing mostly absent. **Median leaf cells** with moderate acute to bulging trigones; marginal cells not differentiated, 16--22 μm where subisodiametric; oil bodies not persistent;

cuticle moderately papillose. **Specialized asexual reproduction** by gemmae rare, brown and purple, exceptionally green in sun, 2-celled, ellipsoid, 9--16 x 16--28 μm . **Sexual condition** dioicous. **Perianth** compressed, mouth dentate.

Restricted to bogs in taiga, also on peaty soil and wet rocks in tundra; 0--2000 m; Greenland; Alta., B.C., Man., N.B., Nfld., N.W.T., N.S., Ont., Que., Sask., Yukon; Alaska, Conn., Maine, Mich., Minn., Mont., N.H., N.Y., Vt., Wis.; Eurasia.

Scapania paludicola is distinct from the other species of sect. *Irriguae* in having dorsal lobes that are decurrent, obcordate, subparallel and crossing far beyond the stem. These characters of *S. paludicola* closely resemble those of *S. uliginosa* of the sect. *Scapania*. See discussion of that species. A minor variant is *Scapania paludicola* var. *rotundiloba* R. M. Schust. ex Konstant. & L. Söderstr., known only from Greenland. It differs in ventral leaf lobes becoming broadly orbicular, dorsal lobes blunt to rounded at apex, leaf margins edentate, and gemmae seldom developing pigmentation in sun-lit sites. A similar taxon is *S. paludicola* var. *viridigemma* R. M. Schuster, known from Greenland, Quebec and New Hampshire, which differs from the typical variety only in gemmae greenish at maturity.

34. *Scapania glaucocephala* (Taylor) Austin, Bull. Torrey Bot. Club 6: 85.1876

Jungermannia glaucocephala Taylor, London J. Bot. 5: 277. 1846; *Scapania saxicola* R. M. Schuster; *S. glaucocephala* var. *saxicola* (R. M. Schuster) Potemkin; *Scapaniella glaucocephala* (Taylor) Evans

Plants 3--10 x 0.85--1.5(--2.25) mm, green to brownish. **Leaves** entire to dentate distally; terminal tooth cell variable, 1--4 times as long as wide; dorsal lobe 0.5--0.75 times the size of ventral, 0.4--0.65 times as wide as long, subtransversely inserted, not extending to distal edge of stem, divergent with it, triangular and pointed to mucronate and apiculate at apex when non-gemmiparous; ventral lobe 0.45--0.65 times as wide as long, subtransversely inserted, blunt to mucronate and apiculate at apex when non-gemmiparous, not hyaline near base margin; keel 0.38--0.65 times the length of ventral lobe, rounded at least basally, moderately arched, wing absent. **Median leaf cells** with small to moderate acute to slightly bulging trigones; marginal cells more or less thick-walled mostly in non-gemmiparous leaves, 16--20(--24) μm where subisodiametric; oil bodies not persistent; cuticle smooth to moderately papillose. **Specialized asexual reproduction** by gemmae, common, brown and reddish brown, at least half are 2-celled at maturity, broadly to narrowly ovoid and ellipsoid, 8--14 x 8--23(--28) μm . **Sexual condition** dioicous. **Perianth** more or less compressed, mouth entire to sinuate-lobed.

Largely xylicolous, mostly on decorticated spruce and fir logs in deep, shaded, humid spruce-fir forests and cedar-spruce swamps, more rarely on sandstone, igneous rocks, and humus; 0--2000 m; Alta., B.C., N.W.T., Ont., Que.; Calif., Mich., Minn., N.H., N.J., N.Y., Vt., Wis.; Eurasia.

An important distinctive character of xylicolous plants of *Scapania glaucocephala* is the frequent production of gemmiparous flagellae with small 2-lobed mostly unbordered leaves. Similar flagellae are characteristic of *S. apiculata*, which is distinct in its uniformly 1-celled gemmae and the absence of thick-walled marginal cells. Saxicolous plants of *S. glaucocephala* (= *S.*

glaucocephala var. *saxicola* (R. M. Schuster) Potemkin (A. D. Potemkin 1999a) usually do not develop gemmiparous flagellae and may produce dentate leaves. A possibly synonymous species known only from New Hampshire, *Scapania calciphila* R. M. Schuster, differs in the cuticle coated with coarse warts and oil bodies 2--4(--5) per cell. The dorsal leaf lobe is somewhat reduced.

35. *Scapania carinthiaca* Lindberg, Rev. Bryol. 7: 77. 1880

Scapania massalongii (K. Müller (Freiburg)) K. Müller (Freiburg)

Plants (1--2--6 x 0.5--1.5(--1.75) mm, green to brown. **Leaves** entire to occasionally dentate distally, terminal tooth cell mostly not over 1.5 times as long as wide; dorsal lobe 0.5--0.75 times the size of ventral, 0.45--0.85 times as wide as long, subtransversely inserted, not extending to far edge of stem, divergent with it, triangular and pointed to mucronate at apex; ventral lobe 0.45--0.7 times as wide as long, subtransversely inserted, triangular and pointed to mucronate at apex, not hyaline near base margin; keel 0.5--0.65 times the length of ventral lobe, rounded basally, acute distally, moderately arched, wing absent. **Median leaf cells** with small acute to large bulging, occasionally confluent trigones; marginal cells thick-walled, subisodiametric to tangentially elongated, 14--18 x 16--24 μm , 12--17 μm where subisodiametric; oil bodies not persistent; cuticle slightly papillose. **Specialized asexual reproduction** by gemmae, common, reddish-brown, largely 1-celled, ovoid, 6--12 x 11--16 μm . **Sexual condition** dioicous. **Perianth** slightly to strongly compressed, mouth entire.

Peaty soil, conglomerate-quartzite and sandstone cliffs; of conservation concern; 0--200 m; Nfld., N.S., Que.; Minn., Wis.; Eurasia.

Scapania carinthiaca is known from five localities in the study area. The report of this species (as *S. massalongii*) from Alaska (W. C. Steere and H. Inoue 1978) is based on material of *S. brevicaulis*. Distinct thick-walled marginal cells is the most convenient character to distinguish *S. carinthiaca* from *S. brevicaulis*.

36. *Scapania apiculata* Spruce, Hepat. Pyrenaicae [Exsicc.] n. 15. 1847

Plants 1.8--5 x 0.5--1.9 mm, green to brownish. **Leaves** entire; dorsal lobe 0.65--0.8 ventral, 0.5--0.7 times as wide as long, subtransversely inserted, not extending to far edge of stem, divergent with it, triangular and sharp-pointed at apex; ventral lobe 0.45--0.67 times as wide as long, subtransversely inserted, triangular and sharp-pointed at apex, not hyaline near base margin; keel 0.6--0.75 times the length of ventral lobe, rounded to acute basally, moderately arched, wing absent. **Median leaf cells** with large bulging to moderate acute trigones; marginal cells not differentiated, 16--20(--24) μm where subisodiametric; oil bodies not persistent; cuticle moderately papillose. **Specialized asexual reproduction** by gemmae, common, red to brown, 1-celled, broadly ovoid, 7--11 x 11--18 μm . **Sexual condition** dioicous. **Perianth** strongly compressed, mouth entire to crenulate.

Moist decaying logs; 0--3000 m; Alta., B.C., Man., N.W.T., N.S., Ont., Que.; Alaska, Maine, Mich., Minn., Mont., N.H., N.Mex., N.Y., Wis.; Eurasia.

The elevational range of *Scapania apiculata* is poorly known. The species is distinct from *S. carinthiaca*, which also produces 1-celled gemmae, in its thin-walled marginal cells and in the strong reduction of the gemmiparous leaves.

37. *Scapania kaurinii* Ryan, Bot. Not. (1889): 210. 1889

Plants 5--30 x 1--3.5 mm, green to brown. **Leaves** entire; dorsal lobe (0.65--0.75--0.85 times the size of ventral, 0.75--1.3 times as wide as long, subtransversely inserted, mostly extending to far edge of stem or slightly beyond it, divergent with stem, obtuse at apex; ventral lobe 0.75--1.15 times as wide as long, arcuately inserted, rounded to obtusely pointed at apex, not hyaline near base margin; keel 0.35--0.55 times the length of ventral lobe, acute, indistinctly to strongly arched, wing mostly narrow, entire. **Median leaf cells** with small acute to moderate slightly bulging trigones; marginal cells not differentiated, 15--20 μm where subisodiametric; oil bodies not persistent; cuticle slightly papillose. **Specialized asexual reproduction** by gemmae rare, green to brown and purple, (1--2)-celled, ovoid, 14--19 x 25--33 μm . **Sexual condition** monoicous (paricous, more rarely autoicous). **Perianth** more or less compressed, mouth lobulate-laciniate to dentate.

Moist rocks, rock detritus, soil; 0--1600 m; Greenland; B.C., N.W.T.; Alaska; Europe (Finland, Norway, n Russia, Sweden); Asia (n Russia).

Scapania kaurinii, when sterile, may be confused with *S. hyperborea* var. *hyperborea*. It differs from the latter in usually having a distinct narrow keel wing (vs. no distinct wing), small acute to moderate slightly bulging trigones, and sharply defined, often 2--3-stratose (vs. weakly defined, mostly 1--2-stratose) cortex. The leaves of *S. kaurinii* are mostly upturned and incurved.

Other References

- Arnell, H. W. 1922. Die schwedischen Arten der Gattungen *Diplophyllum* and *Martinellia*. Pflanzengeographische Skizzen. Göteborg. 82 pp.
- Borovichev E., Fedosov V., Vilnet A. A. 2016. An unexpected record of European liverwort *Scapania aspera* (Scapaniaceae, Jungermanniopsida, Marchantiophyta) in the East Siberia. *Cryptogamie, Bryologie* 37: 445--454.
- Bryhn, N. 1906. Bryophyta in itinere polari norvagogorum secundo collecta. Hepaticae. Rept. 2nd Norwegian Arctic Exped. in the "Frahm" 1898--1902, 2(11): 1--52.
- Damsholt, Kell. 2002. Illustrated flora of Nordic liverworts and hornworts. Lund, Sweden: Nordic Bryological Society.
- Damsholt, K. and D. Long. 1981. The relationship between sect. *Compactae* (K. Müll.) Buch and subgen. *Jensenia* S. Arnell of the genus *Scapania* (Dum.) Dum. (Hepaticae). *Lindbergia* 7: 103--108.
- de Roo, R. T., T. A. Hedderston, and L. Söderström. 2007. Molecular insights into the phylogeny of the leafy liverwort family Lophoziaceae Cavers. *Taxon* 56(2): 301-314.

- Duell, R. 1983. Distribution of the European and Macaronesian Liverworts (Hepaticophytina). *Bryol. Beitr.* 2: 1--115.
- Frye, T. C. and L. Clark 1937--1947. Hepaticae of North America. Univ. Wash. Publ. Biol. 6: 1--1022.
- Grolle, R. and D. G. Long. 2000. An annotated check-list of the Hepaticae and Anthocerotae of Europe and Macaronesia. *J. Bryol.* 22: 103--140.
- Hentschel, J., J. A. Paton, H. Schneider, and J. Heinrichs. 2007. Acceptance of *Liochlaena* Nees and *Solenostoma* Mitt., the systematic position of *Eremonotus* Pearson and notes on *Jungermannia* L. s.l. (Jungermanniiidae) based on chloroplast DNA sequence data. *Plant Systematics and Evolution* 268: 147--157.
- International Code of Nomenclature for algae, fungi, and plants (Melbourne Code) adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. Koeltz Scientific Books, 2012.
- Paton, J. A. 1999a. Lophoziaceae. Pp. 162--255 In: The liverwort flora of the British Isles. Colchester, UK: Harley Books.
- Paton, J. A. 1999b. Scapaniaceae. Pp. 337--385 In: The liverwort flora of the British Isles. Colchester, UK: Harley Books.
- Polunin, N. 1947. Hepaticae. In: Botany of the Canadian Eastern Arctic. II. Thallophyta and Bryophyta. *Bull. Natl. Mus. Canada* 97: 491--512.
- Potemkin, A. D. 1995. Contribution to the knowledge of the liverworts of North America. *Fragm. Flor. Geobot.* 40(1): 323--338.
- Potemkin, A. D. 1999a. An analysis of the practical taxonomy of some critical northern species of *Scapania* (Scapaniaceae, Hepaticae). *Bryologist* 102: 32--38.
- Potemkin, A. D. 1999b. *Scapania lingulata* from Nevada---a new puzzle of the sect. *Curtae* (Scapaniaceae, Hepaticae). *Hausknechtia Beiheft* 9: 291--298.
- Schuster, R.M. 1958. Notes on Nearctic Hepaticae XIII. The genus *Tritomaria* (Lophoziaceae) in Arctic Canada. *Canad. Jour. Bot.* 36: 269--288.
- Schuster, R. M. 1969. Lophoziaceae. Pp. 218--806 In: Hepaticae and Anthocerotae of North America east of the hundredth meridian. Vol. 2. New York: Columbia University Press.
- Schuster, R. M. 1974. Scapaniaceae. Pp. 171--617 In: Hepaticae and Anthocerotae of North America east of the hundredth meridian. Vol. 2. New York: Columbia University Press.
- Schuster, R. M. 1988. The Hepaticae of South Greenland. *Beiheft zur Nova Hedwigia* 92: 1--255.
- Schuster, R. M. and K. Damsholt 1974. The Hepaticae of West Greenland from ca.66° N. to 72°N. *Meddelelser om Groenland.* 199(1): 1--373.
- Shaw, B., B. Crandall-Stotler, J. Vána, R. E. Stotler, M. von Konrat, J. J. Engel, E. C. Davis, D.G. Long, P. Sova, and A. J. Shaw. 2015. Phylogenetic relationships and morphological evolution in a major clade of leafy liverworts (Phylum Marchantiophyta, Order Jungermanniales): Suborder Jungermanniiineae. *Syst. Bot.* 40: 27-45.
doi:10.1600/036364415X686314
- Shlyakov, R. N. 1980. Lophoziaceae. Pp. 1--164. In: Liverworts of the USSR part 3 [in Russian]. Leningrad: Nauka.
- Shlyakov, R. N. 1981. Scapaniaceae. Pp. 109--195. In: Liverworts of the USSR part 4 [in Russian]. Leningrad: Nauka.
- Söderström, L., R. de Roo, and T. Hedderson. 2010. Taxonomic novelties resulting from recent reclassification of the Lophoziaceae/ Scapaniaceae clade. *Phytotaxa* 3: 47--53.

- Söderström, L., A. Hagborg, M. von Konrat, S. Bartholomew-Began, D. Bell, L. Briscoe, E. Brown, D. C. Cargill, D. P. Costa, B. J. Crandall-Stotler, E. D. Cooper, G. Dauphin, J. J. Engel, K. Feldberg, D. Glenney, S. R. Gradstein, X. He, J. Heinrichs, J. Hentschel, A. L. Ilkiu-Borges, T. Katagiri, N. A. Konstantinova, J. Larrain, D. G. Long, M. Nebel, T. Pócs, F. Puche, E. Reiner-Drehwald, M. A. M. Renner, A. Sass-Gyarmati, A. Schäfer-Verwimp, J. G. Segarra Moragues, R. E. Stotler, P. Sukkharak, B. M. Thiers, J. Uribe, J. Váña, J. C. Villarreal, M. Wigginton, L. Zhang, and R.-L. Zhu. 2016. World checklist of hornworts and liverworts. *Phytokeys* 59: 1--828.
- Stotler, R. E. and B. Crandall-Stotler. 2017. A synopsis of the liverwort flora of North America north of Mexico. *Annals of the Missouri Botanical Garden* 102: 574--709. doi: 10.3417/2016027
- Steere, W. C. and H. Inoue 1978. The Hepaticae of Arctic Alaska. *J. Hattori Bot. Lab.*44: 251--345.
- Withering, W. A. 1776. *Botanical arrangement of all the vegetables naturally growing in Great Britain*. Vol. 2. Birmingham. Pp. 385--838.
- Zehr, D. R. 1980. An assessment of variation in *Scapania nemorosa* and selected related species. *Bryophyt. Biblioth.* 15: 1--140. Berlin.