24. LEUCOBRYACEAE Schimper

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Plants in small to large cushions, white to pale green, glaucous, grayish or pale brown. **Stems** erect, branching, central strand absent or poorly developed. **Leaves** thick, consisting mostly of an expanded costa, distal part of leaf (limb) linear, ligulate or lanceolate, ± tubulose, spreading from a narrow base (sheath); costa consisting of 2 to several layers of enlarged empty, hyaline, thin-walled, porose cells (leucocysts) enclosing a central layer of small, green cells (chlorocysts); unistratose lamina restricted to leaf base, consisting of very narrow, delicate, hyaline, quadrate to oblong or linear cells. **Sexual condition** dioicous, pseudautoicous, or autoicous. **Seta** terminal, straight. **Capsule** erect to inclined, symmetric or asymmetric, often strumose; operculum long-rostrate, often longer than urn; annulus present or absent; peristome teeth 8–16, entire or divided 1/2 their length, articulate. **Calyptra** cucullate or mitrate, smooth, rarely fringed at base. **Spores** spherical.

Genera 8, species ca. 155 (1 genus, 2 species in the flora): worldwide except Antarctica in temperate and tropical areas.

Species of Leucobryaceae are characterized by plants with thick, whitish leaves consisting mostly of expanded costa and narrow basal lamina. The actual number of genera in this family is uncertain. Current attributions range from one (A. Eddy 1988+, vol. 2) to four (D. H. Vitt 1982) to eight (H. Robinson 1985). Because of its peculiar peristome, *Octoblepharum* is placed in the Octoblepharaceae by Eddy and in the Leucophanaceae by W. D. Reese (pers. comm.). The Leucobryaceae have been sometimes included in the Dicranaceae because of similar costal modifications in *Brothera*, *Campylopus,* and *Paraleucobryum* and a peristome structure identical with that of *Dicranum* (M. R. Crosby and R. E. Magill 1977). Robinson suggested that in large part the characteristic pale color of *Leucobryum* is caused by air bubbles in the leucocysts, and the presence of air in the leaf is assumed characteristic of the Leucobryaceae. Furthermore, he concluded that "such bubbles are necessary for the function of the chlorocysts, which are remote from the surface of the leaf, and which could not properly exchange gases if the leucocysts were all filled with water."

SELECTED REFERENCES Robinson, H. 1985. The structure and significance of the leucobryaceous leaf. Monogr. Syst. Bot. Missouri Bot. Gard. 11: 111–120. Robinson, H. 1990. A functional evolution of the Leucobryaceae. Trop. Bryol. 2: 223–237. Yamaguchi, T. 1993. A revision of the genus *Leucobryum* (Musci) in Asia. J. Hattori Bot. Lab. 73: 1–123.

1. LEUCOBRYUM Hampe, Linnaea 13: 42. 1839 • [Greek *leukos*, white, and *bryon*, moss]

Plants in compact to loose cushions or turfs. **Stems** 0.5–15 cm. **Leaves** crowded, limbs lanceolate or subulate-lanceolate and concave to subtubulose, erect, spreading, reflexed to flexuose or falcate-secund, little changed when dry, spreading from an oblong-obovate to elliptic sheath; costa consisting of 1–4 layers of abaxial and 1–4 layers of adaxial leucocysts that enclose a central layer of quadrate chlorocysts; inner walls of leucocysts with single pores; external pores often present on the abaxial surfaces of the cell walls of leucocysts in the apical and basal regions of leaves. **Specialized asexual reproduction** by small, caducous, leaf-like gemmae, and by leaves with rhizoids borne adaxially on exposed chlorocysts at leaf apex. **Sexual condition** pseudautoicous, with dwarf male plants growing on tufts of tomentum or leaves of female plants. **Seta** 1(–2). **Capsule** inclined, asymmetric, plicate when dry, often strumose; operculum long-rostrate; annulus usually absent; peristome teeth 16, divided 1/2 their length, longitudinally pitted-striolate proximally, papillose distally. **Calyptra** cucullate, often split incompletely to base, which clasp the tip of seta until capsule mature. **Spores** yellowish or brownish, nearly smooth to minutely papillose.

Species ca. 122 (2 in the flora): worldwide except Antarctica in temperate and tropical areas.

Based on an analysis of ten separate characters of the leucobryoid leaf, J. Burch (1997) suggested that *Leucobryum* may not be phylogenetically homogeneous, but that possibility remains to be evaluated. The external pores of the leucocysts can be demonstrated by staining with safranin.

1. Plants in low, compact cushions or turfs; stems less than 1 cm (rarely to 4.5 cm); leaves 2–4(–6) mm, limb subtubulose, erect to wide-spreading, straight, shorter than (rarely equal to) length of sheath . . . . . 1. *Leucobryum albidum*
1. Plants in tall, compact cushions or turfs; stems mostly 1–12.5 cm (rarely shorter); leaves mostly 3–9 mm, limb concave to subtubulose, erect-spreading, sometimes falcate-secund, 1–2(–3) times length of sheath . . . . . 2. *Leucobryum glaucum*

1. Leucobryum albidum (P. Beauvois) Lindberg, Öfvers. Kongl. Vetensk.-Akad. Förh. 20: 403. 1863

Dicranum albidum P. Beauvois, Prodr. Aethéogam., 52. 1805

Plants in low, compact cushions or turfs. **Stems** less than 1 cm tall (rarely to 4.5 cm). **Leaves** 2–4 (–6) mm, limb subtubulose, erect to wide-spreading, straight, apex apiculate, entire, speading from oblong-obovate sheath, shorter than (rarely equal to) the length of the sheath; costa in transverse section near base showing lateral, thicker regions composed mostly of 2(–3) layers of enlarged leucocysts on both sides of the central layer of chlorocysts, and a central, thinner region composed of 1 layer of smaller leucocysts on both sides of the chlorocyst layer; lamina narrow, 8–11 cells wide. **Specialized asexual reproduction** by small leaf-like gemmae on minute, forked branches at stem tip or on pseudopodium-like branches and by caducous leaves with rhizoids at leaf apex. **Seta** 8–12 mm, brown to reddish. **Capsule** strongly inclined and curved when dry and empty, sometimes slightly strumose, 1.2–1.8 mm, red to reddish brown; operculum 1–1.3 mm; peristome teeth dark red. **Spores** minutely papillose, 11–16 µm.

Capsules mature Aug–Jan. Moist humus, sandy soil, rotting logs and stumps, tree bases, hardwood trees, pine and palms, forests, bogs, and swamps; low to moderate elevations (0–1000 m); Ont.; Ala., Ark., Conn., Del., D.C., Fla., Ga., Ill., Ind., Kans., Ky., La., Maine, Md., Mass., Mich., Minn., Miss., Mo., N.H., N.J., N.Y., N.C.,

Ohio, Okla., Pa., R.I., S.C., Tenn., Tex., Vt., Va., W.Va., Wis.; Mexico (Tamaulipas); West Indies; Bermuda; Central America.

Leucobryum albidum characteristically occurs in small, low cushions, usually no more than 10 cm in diameter, and frequently bears sporophytes. Of the 1035 collections examined, 632 (61 percent) had sporophytes. *Leucobryum albidum* is sometimes difficult to separate from small plants of *L. glaucum*. Some authors have used the number of leucocysts, as seen in transverse section, on both sides of the chlorocyst layer on thicker, lateral regions of costa to separate these species. However, this character varies widely on plants from the same colony and even on different sides of the same leaf. There is also no consistent pattern for these species across the geographical range, and correlation with other characters such as stem height and length of limb to length of sheath is inconclusive. The most satisfactory criteria for recognizing *L. albidum* are its generally compact, short cushions and leaves 2–4 mm with reflexed limb usually shorter than the sheath. E. Patterson et al. (1998) in a study of *Leucobryum* from a limited area near Durham, North Carolina, using nuclear ribosomal DNA extracts from plants of various sizes, demonstrated that two haplotyes were present, and that *L. albidum* (small plants) is genetically discontinuous with *L. glaucum* (large plants). *Leucobryum incurvifolium* Müller Hal. [= *Terrestria incurvifolia* (Müller Hal.) W. L. Peterson] was reported from Florida (W. L. Peterson and A. J. Sharp 1980). However, the two collections cited from Florida appear to be nothing more than a variation of *L. albidum*. They do not have the distinct cucullate, hyaline-apiculate leaf tips characteristic of *L. incurvifolium* (Peterson 1994).

2. Leucobryum glaucum (Hedwig) Ångström in E. M. Fries, Summa Veg. Scand. 1: 94. 1845 F

Dicranum glaucum Hedwig, Sp. Musc. Frond., 135. 1801

Plants in tall, compact cushions or turfs. **Stems** 1–12.5 cm (rarely shorter). **Leaves** 3–9 mm, limb concave to subtululose, erect or erect-spreading, sometimes falcate-secund, apex acute or apiculate, usually ± serrulate at the tip, spreading from oblong-obovate sheath, 1–2(–3) times the length of sheath; costa in transverse section near base showing lateral, thicker regions composed mostly of 2–3(–4) layers of enlarged leucocysts on both sides of the central layer of chlorocysts and a central, thinner region composed of 1 layer of smaller leucocysts adaxial to and 2 layers abaxial to the chlorocysts (or vice versa), occasionally with only 1 layer of leucocysts on both sides of the chlorocysts; lamina narrow, 5–11 cells wide. **Specialized asexual reproduction** by clusters of small caducous leaf-like gemmae at stem tip and by leaves with rhizoids at apex. **Seta** 8–18 mm, reddish. **Capsule** strongly inclined and curved when dry and empty, usually strumose, 1.5–2 mm, red to reddish brown; operculum 1.5–2 mm; peristome teeth dark red. **Spores** nearly smooth to minutely papillose, 13–18 µm.

Capsules mature Aug–Dec. Humus, soil, rotting logs and stumps, tree bases, and rock ledges, forests, bogs, and swamps; low to high elevations (0–1800 m); Alta., Man., N.B., Nfld. and Labr. (Nfld.), N.S., Ont., P.E.I., Que.; Ala., Ark., Conn., Del., D.C., Fla., Ga., Ill., Ind., Iowa, Kans., Ky., La., Maine, Md., Mass., Mich., Minn., Miss., Mo., N.H., N.J., N.Y., N.C., Ohio, Okla., Pa., R.I., S.C., Tenn., Tex., Vt., Va., W.Va., Wis.; Eurasia; Atlantic Islands (Canary Islands, Madeira).

The collection from Alberta (*Drummond's Musci Americani 89*, TENN) is probably incorrectly labeled as to locality.

Large, tall cushions distinguish *Leucobryum glaucum* and under favorable circumstances some cushions may exceed 1 m in diameter. The separation of smaller, shorter plants from *L. albidum* is difficult. The use of the number of layers of leucocysts on both sides of the chlorocysts is highly variable and not a reliable distinguishing feature. The ratio of length of the sheath to the length of the limb provides the most consistent way to separate *L. glaucum* from *L. albidum*. Sporophytes are infrequently observed. Of 1933 collectons examined, 308 (16 percent) had sporophytes. Most of the plants with sporophytes were from collections located north of the Ohio River. *Leucobryum antillarum* Bescherelle var. *antillarum* has been reported from the Coastal Plain of the United States based upon plants that had only 1 layer of leucocysts on both sides of the chlorocysts across a wide section of the median portion of the leaf as seen in transverse section near the base. However, this character is quite variable and not even consistent in *L. antillarum* (H. A. Crum and L. E. Anderson 1981, vol. 2). Also, plants from the coastal plain do not show the prorate cells on the lateral wings of the lamina that are present in the type material of *L. antillarum*.