The genus *Leucobryum* (Musci: Leucobryaceae) in Maine

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The species of *Leucobryum* have thick, glaucous to whitish leaves that consist mostly of an expanded costa. The costa is differentiated into outer layers of enlarged, hyaline leucocysts and a central layer of smaller, green chlorocysts. Since a similar costal modification is found in the Dicranaceae (i.e., *Campylopus*, *Brothera*, *Paraleucobryum*) and the peristomes of *Leucobryum* and *Dicranum* are identical the two families are sometimes merged. However, many recent treatments (Crum & Anderson 1981, Ireland 1982, Walther 1983, Vitt 1984, Robinson 1985, Anderson, *et al.* 1990, Eddy 1990, Allen 1994, Peterson 1994, Churchill & Linares 1995) recognize both families. Robinson (1985, 1990) attributed basic structural and functional differences to the leucobryaceous leaf and on this basis redelimited the family. The important functional aspect of the leucobryaceaeous leaf involves its ability to generate and hold air within the leucocysts. Robinson suggests that "such bubbles are necessary for the photosynthesis in 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." Although many authors include the genus *Octoblepharum* (not found in Maine) in the Leucobryaceae, Reese (1998) places this genus in the Leucophanaceae because of its peculiar peristome.

Leaf size, shape and stature are important taxonomic characters in *Leucobryum*, as also are characters found in the reduced leaf lamina and the number of leucocyst layers at the base of the leaves. In determining the leucocyst-layer number it is necessary to make leaf cross-sections at the extreme leaf base (first six sections). The glaucous-green to whitish color of the plants makes the use of a contrast enhancing stain (e.g., crystal-violet) helpful. The pores of the leucocysts can be demonstrated by staining with safranin.

Leucobryum Hampe, Flora 20: 282. 1837.

Plants in compact to loose cushions or mats, white to pale green, glaucous, grayish or pale brown. Stems simple or forked to irregularly branched, from 0.5–15 cm high; central strand of small, thin-walled, frequently fugacious cells present or absent; rhizoids red-brown, on stems and from apex of leaves. Leaves crowded, consisting mostly of a broad costa, limb 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, apex acute or obtuse and cucullate; margins incurved above, entire, or weakly denticulate at the apex; costa as seen in transverse section near the base consisting of 1–4 layers of abaxial and 1–4 layers of adaxial leucocysts, with single pores in their internal walls that enclose a central layer of quadrate chlorocysts; external pores often present on the abaxial surfaces of the cell walls of leucocysts in apical and basal regions of leaves; leaf lamina present from leaf base to mid-leaf, consisting of a narrow (2-12 rows of cells) marginal band of hyaline, linear, long-rectangular, short-rectangular or quadrate, variably porose, firm to lax walled, cells. Asexual reproduction by small caducous leaf-like gemmae and by leaves with rhizoids borne adaxially on exposed chlorocysts at the leaf apex. Pseudautoicous; male plants dwarfed, growing on tufts of tomentum or leaves of female

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plants. Setae elongate, 1 or occasionally 2 per perichaetia. Capsules inclined, asymmetric, rarely erect and symmetric, often plicate when dry, often strumose, stomata absent; opercula long-rostrate; annulus mostly nonrevoluble; peristome teeth 16, divided ½ their length, vertically pitted-striolate below, papillose above. Calyptrae cucullate, often split incompletely to the base which clasps the tip of seta until capsule matures. Spores yellowish or brownish, nearly smooth to minutely papillose. n = 6–11 (Fritsch 1991).

The name *Leucobryum* combines the Greek *leuco*, white and *bryum*, a moss. The characteristic pale color of *Leucobryum* is caused by air bubbles in the leucocysts (Robinson 1985). In Maine *Leucobryum* is a common woodland moss that often occurs in extensive mats. The genus can be recognized by its cushion-like growth form, and thick, whitish leaves. *Leucobryum* is sometimes called the "pin cushion moss" because of its habit, and indeed large mats of it make a comfortable woodland-seat. But beware, *Leucobryum* absorbs and holds large amounts of water for some time after a rain storm; Ireland (1982) relates that in Quebec it is sometimes called "Mother-in-law Cushion" because "... if you are out for a walk in the woods with your mother-in-law you should invite her to sit down to rest on a cushion of *Leucobryum* which has a dry appearance but frequently contains great quantities of water."

There are about 122 species of *Leucobryum* in the temperate and tropical regions of the world. Recently, Burch (1997) suggested the genus may be polyphyletic, but that possibility remains to be evaluated. Only two species are recognized in North America (Redfearn 1999), and these are not always easy to separate. Characters such as cushion height, leaf limb to sheath ratio, leaf length, and the number of leucocyst layers above and below the chlorocysts in transverse leaf sections near the base have been used to separate the species. The latter character is given great consideration in many floras. However, the number of leucocysts above and below the chlorocysts is too variable, e.g, on plants from the same colony and even on different sides of the same leaf, to be consistently used in separating the species. The best ways to separate the North American species of *Leucobryum* are by cushion height, leaf length, and the ratio of leaf limb to sheath length. Although both species have the same sexual system (dioicous with dwarf males) they differ in their frequency of sexual reproduction. In North America 16 % of the collections of *L. glaucum* examined had sporophytes, while 61% of the collections of *L. albidum* contained sporophytes. (Redfearn 1999).

Although the two North American species of *Leucobryum* are concentrated in different regions (*L. albidum* in the southeast; *L. glaucum* in the northeast) their ranges overlap extensively. Morphological intergradation between them is so great that one could recognize them as varieties rather than species. Patterson, Boles, & Shaw (1998), however, using nuclear ribosomal DNA analysis, demonstrated the presence of two distinct, genetically discontinuous haplotypes, one corresponding to *L. glaucum* the other to *L. albidum*.

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

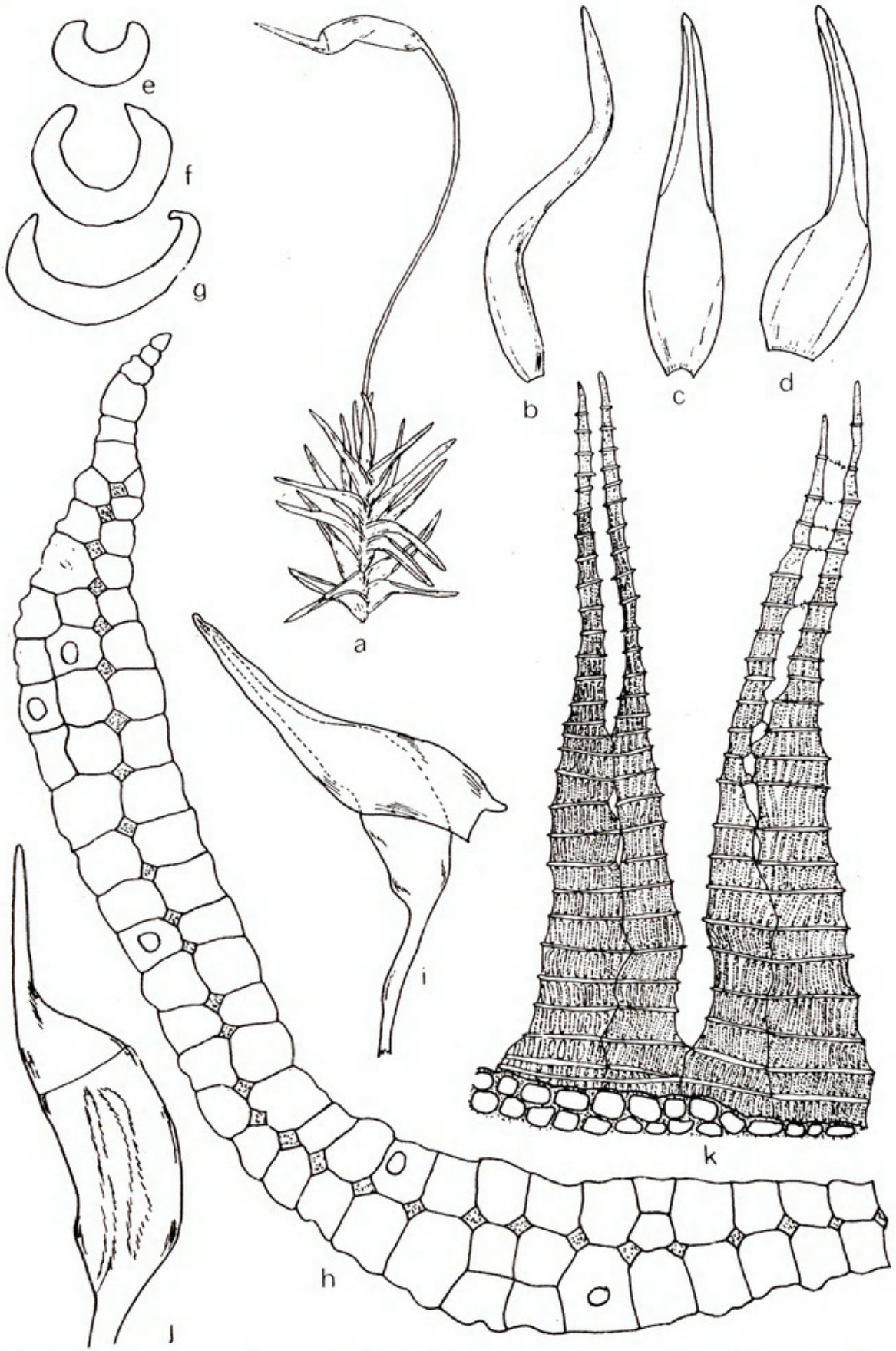

Figure 1. *Leucobryum albidum*. a. Habit. b–d. Leaves. e–g. Transverse sections of leaf, upper tubulose portion to upper sheath. h. Transverse section of lower sheath of leaf . i. Capsule with calyptra. j. Capsule with operculum. k. Peristome.

Leucobryum albidum (Brid. *ex* P. Beauv.) Lindb., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 20: 403. 1863.
Dicranum albidum Brid. *ex* P. Beauv., Prodr. Aethéogam. 52. 1805.

Plants in low, compact cushions or mats. Stems less than 1 cm tall (rarely to 4.5 cm), Leaves 2–4(–6) mm long, limb subtubulose, erect to wide-spreading, straight, apex apiculate, broadly acute to obtuse, entire, spreading from an 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 above and below the central layer of chlorocysts, and a central, thinner region composed of 1 layer of smaller leucocysts above and below chlorocysts; lamina narrow, 8–11 cells wide, cells quadrate to rectangular. Asexual reproduction by small leaf-like gemmae on minute, forked branches at stem tip or on pseudopodium-like branches and by leaves bearing rhizoids at leaf apex. Setae 8–12 mm long, brown to reddish. Capsules strongly inclined and curved when dry and empty, sometimes slightly strumose, 1.2–1.8 mm long, red to reddish-brown; opercula 1–1.3 mm long; peristome teeth dark red. Calyptrae 2 mm long. Spores minutely papillose, 11–16 μm. $n = 6$ (Anderson and Bryan 1958).

On moist shaded soil. In Maine known from Cumberland (*Wilson* NY), Hancock (*Bold 208* SMS, UT), Oxford (*J. A. Allen* NY), Sagadahoc (*Eckel* MICH), and Washington (*Holmes 111* MO) Counties.

Leucobryum albidum, a common southeastern North America species, is known in Maine from only a few, mostly coastal, localities. It is a small moss with plants that grow as compact, short cushions that are no more than 10 cm in diameter. The leaves of *L. albidum* often have rounded to obtuse leaves. Its smaller size is usually enough to separate it from *L. glaucum*. However, *L. glaucum* is extremely variable in size and at the smaller end of its range, *L. glaucum* and *L. albidum* intergrade. The best way to recognize *L. albidum* is by its leaves that have a reflexed limb that is usually shorter than the leaf sheath. Of the 5 collections examined from Maine, 2 (40%) had plants with sporophytes.

Leucobryum glaucum (Hedw.) Ångstrom, Summ. Veg. Scand. 1: 94. 1846.
Dicranum glaucum Hedw., Sp. Musc. Frond. 135. 1801.

Plants in tall, compact cushions or mats. Stems 1–12.5 cm tall (rarely shorter). Leaves 3–9 mm long, limb concave to subtubulose, erect or erect-spreading, sometimes falcate-secund, apex acute or apiculate, usually ± serrulate at the tip, spreading from an 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 above and below the central layer of chlorocysts and a central, thinner region composed of 1 layer of smaller leucocysts above and 2 layers below chlorocysts (or vice versa), occasionally with only 1 layer of leucocysts above and below chlorocysts; lamina narrow 5–11 cells wide, cells quadrate to rectangular. Asexual reproduction by clusters of small caducous leaf-like gemmae at stem tip and by leaves bearing rhizoids at apex. Setae 8–18 mm long, reddish. Capsules strongly inclined and curved when dry and empty, usually strumose, 1.5–2 mm long, red to reddish brown; opercula 1.5–2 mm long, red to reddish-brown; peristome teeth dark red. Calyptrae ca. 2 mm long. Spores nearly smooth to minutely papillose, 13–18 μm.

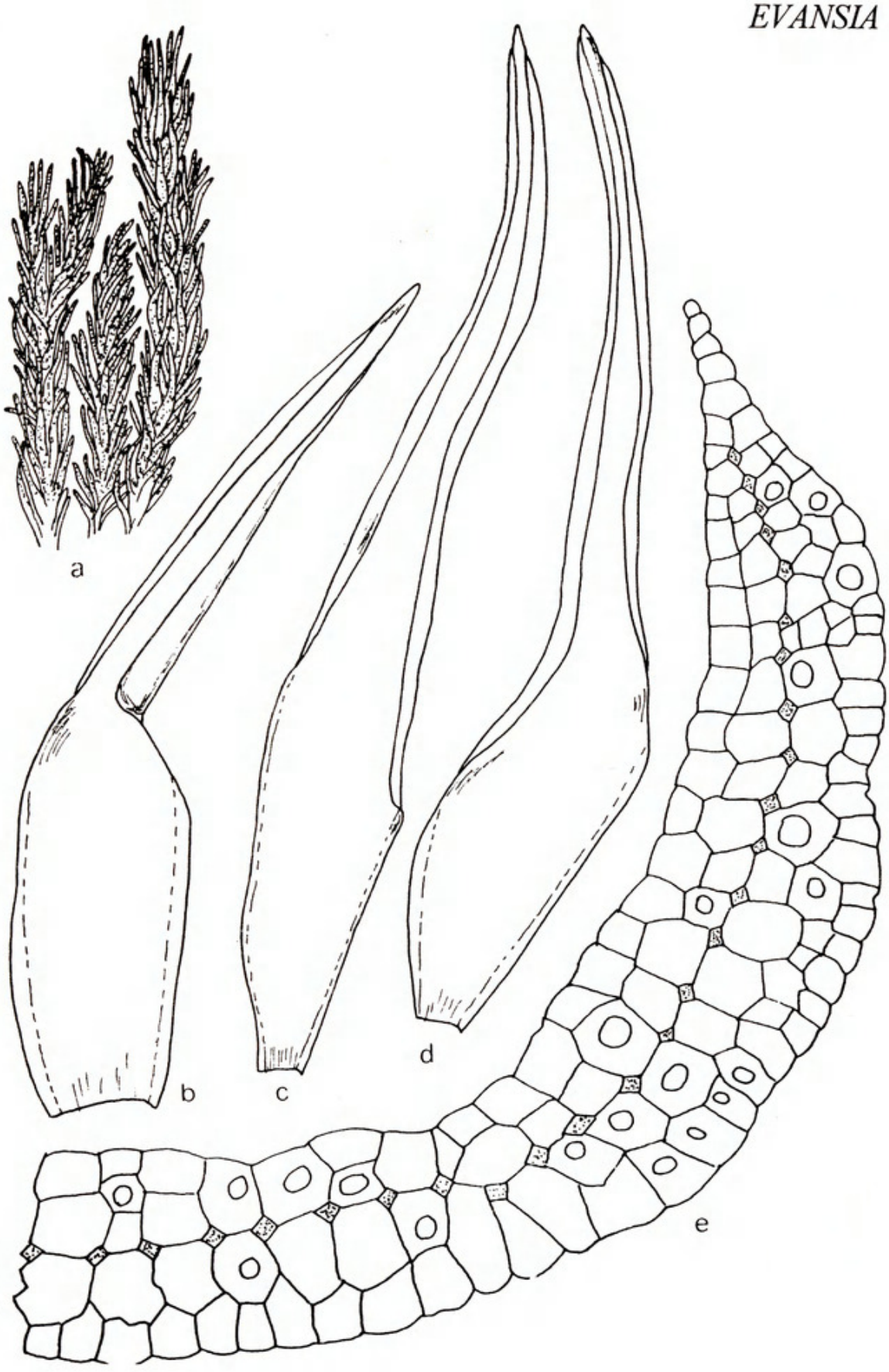

Figure 2. *Leucobryum glaucum.* a. Habit. b–d. Leaves. e. Transverse section of lower sheath of leaf.

On shaded to open humus, soil, rotting logs and stumps, tree bases, and rock ledges in forests and bogs. In Maine known from Androscoggin (*Allen 14664* MO), Aroostook (*Allen 16445* MO), Cumberland (*Allen 6027* MO), Franklin (*Allen 10300* MO), Hancock *(Redfearn 37739 MO*), Kennebec (*Allen 10121* MO), Knox *(Allen 15802* MO), Lincoln (*Allen 15892* MO), Oxford (*J. A. Allen* MO), Penobscot (*Merrill 23* MO, NY), Piscataquis (*Merello 27* MO), Sagadahoc (*Allen 16774* MO), Somerset (*Allen 9370* MO), Waldo (*Allen 10367* MO), Washington (*Pedano 339* MO), and York (*Allen 13059* DUKE, MO, NY) Counties.

Leucobryum glaucum is the common species of *Leucobryum* in Maine. It often grows in extensive, tall cushions that under favorable circumstances may exceed 1 meter in diameter. Normally, the separation of *L. glaucum* from *L. albidum* is not difficult because *L. glaucum* is much larger in size. But, newly established cushions or plants growing in stressed habitats are smaller, shorter and closely approach those of *L. albidum*. Many past treatments of *Leucobryum* relied on the different number of layers of leucocysts above and below the chlorocysts to separate them. This feature is, however, highly variable and will not reliably distinguish the two species. The length ratio of leaf sheath to leaf limb provides the most consistent way to separate *L. glaucum* from *L. albidum.* Of the 58 collections examined from Maine only 4 (6%) had plants with sporophytes. This is a lower percentage than for *L. glaucum* in North America where 16% of collections examined had sporophytes (Redfearn 1999).

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