### The genus Sphagnum sections Sphagnum, Rigida, Squarrosa, and Isocladus (Musci: Sphagnaceae) in Maine

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#### Sphagnum L., Sp. Pl. 1106. 1753.

Isocladus Lindb., Öfvers. Förh. Kongl. Svenska Vetensk ..- Akad. 19: 133. 1862.

Plants coarse and robust to slender and delicate, mostly growing in wet habitats, particularly in bogs and fens, sometimes on moist to wet soils and rocks, forming blankets, mounds, cushions, hummocks, and often submerged with capitulum emergent in pools and lake margins. Stem and branch leaves nearly always differentiated, but hemi-isophylly common in most species in which stem leaves resemble branch leaves in varying degrees of shape and structure. Cortical cells of stem, rarely undifferentiated, usually consisting of 1-several layers of large, hyaline, empty, thin-walled cells, sometimes fibrillose and porose surrounding a wood cylinder consisting of thin-walled prosenchymatous cells becoming thicker walled toward the outside; stem leaves usually more distantly arranged than branch leaves, generally lingulate, extensively resorbed on the outer surface, finely fringed at the margins. Branches usually in spirally arranged fascicles of two or more divergent or spreading branches and two or more pendent or hanging branches, usually becoming crowded at the stem apex into a noticeable capitulum. Stem and branch leaves ecostate, unistratose, consisting of a network of narrow, elongated green cells completely surrounded by large, rhomboidal, empty, hyaline cells, stem leaf hyaline cell walls typically without pores and fibrils; branch leaf hyaline cell walls with at least some pores, often many, and with one exception, round or elliptic, ring-shaped or spiral fibril bands. Dioicous or monoicous. Perichaetial leaves much larger than stem or branch leaves: leaves of antheridial branches generally colored, scarcely differentiated, antheridia globose, on long stalks, produced singly in leaf axils. Capsules globose, operculate, without annulus or peristome, borne on an elongated gametophytic pseudopodium, attached by a large foot, sessile to generally elevated above the perichaetial leaves, becoming brown to black when mature; exothecial cells usually with scattered pseudostomata, consisting of paired guard cells but lacking an opening, more numerous toward the base, columella dome-shaped, overarched by the spore sac; spores triradiate with conspicuous ridges, smooth to roughened, explosively ejected a short distance, leaving the capsule cylindrical or, with age, somewhat urceolate. Chromosome number n = 19 or 38, + 0variable numbers of m-chromosomes.

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Crum's (1984) richly illustrated Flora of North American *Sphagnum* is an excellent reference work and is most helpful in identifying species. The present treatment draws heavily from this and other works, especially Andrews (1913), Crum & Anderson (1981), Andrus (1980), and Daniels & Eddy (1985).

Sphagnum is taxonomically a difficult group. Part of the difficulty in naming Sphagnum collections is technical: in order to work through many keys the plants must be extensively dissected, stems and branches examined in cross section as well as in surface view, and cross-sections made of stem and branch leaves. Many of Sphagnum's technical features, especially the pores, are more easily seen when the leaves and stems are lightly stained. When working with Sphagnum the importance of making good leaf cross sections, which should be made in the upper  $\frac{1}{2}-\frac{2}{3}$  of the leaf, cannot be overemphasized.

#### Key to Sphagnum sections

1. Branch leaves without fibril bands 4. Sphagnum section Isocladus
1. Branch leaves with fibril bands
2. Fascicles containing 6-8 branches Sphagnum section Polyclada
2. Fascicles containing less than 6 branches
3. Branch leaves with a resorption furrow along the margins (best viewed in cross
section)
3. Branch leaves without a resorption furrow
4. Branch leaves strongly cucullate, roughened on back near the apex;
stem and branch cortex fibrillose, sometimes faintly so
4. Branch leaves not or only slightly cucullate, not roughened on back
near the apex; stem and branch cortex efibrillose
5. Branch leaf green cells in cross section more broadly exposed on the inner
surface
5. Branch leaf green cells in cross section enclosed or more broadly exposed on
the outer surface
6. Plants without a distinct capitulum; branches in irregular fascicles of
1–3, loosely arranged around the stem
6. Plants with a distinct, bushy capitulum; branches in regular fascicles
of 3-5, spirally arranged around the stem
7. Branch leaf hyaline cells with pores usually restricted to the ends and corners,
not in bead-like rows along the commissures
Sphagnum section Hemitheca
7. Branch leaf hyaline cells with numerous small pores arranged in bead-like
rows or scattered along the commissures
Sphagnum section Subsecunda (in part)

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8. Branch leaf green cells rectangular or slightly trapezoidal in cross
Scenon, exposed about equally on both surfaces
8 Branch leaf green cells triangular to transgidal surged man
either the inner or outer surface
O Described to the miler of outer surface
9. Branch leaf green cells exposed more on the inner surface
9. Branch leaf green cells exposed more on the outer surface
10. Stem terminal bud prominent. Branch leaves at middle with hyaline
cell pores numerous, greater than 15 µm in diameter; walls of
the hyaline cells adjacent to the green cells faintly papillose
10. Stem terminal bud not conspicuous. Branch leaves at middle with
hyaline cell pores various, less than 12 µm in diameter; walls of
the hyaline cells adjacent to the green cells smooth

## 1. Sphagnum section Sphagnum L., Sp. Pl. 1106. 1753.

Plants normally fairly large, capitula distinct with turgid, pointed or blunt branches, found in wet places in cushions, hummocks, mats, carpets, and rocky shelves, both in open and shaded areas. Stems generally stout, greenish to black, cortical cells large, square, rectangular, or multi-sided, generally in 3-4 layers, outer walls of the outer layer usually fibrillose with pale, delicate to strong, closely arranged fibrils, with 1-10, rarely more, fairly large, generally circular pores; inner cortical cells usually with widely spaced, thin fibrils, the innermost walls adjacent to the wood cylinder sometimes with strong, closely spaced, striate fibrils. Stem leaves large, lingulate to ligulate, flat to slightly concave, with a fringed border due to partial resorption of cells at the margin, both outer and inner walls of hyaline cells partially or almost completely resorbed. Branches stout, often tumid, pointed, with closely overlapping leaves when dry; cortical cells fibrillose, branch leaves broadly ovate, deeply concave, and cucullate, rough on back near apex because of extreme resorption of the hyaline cells; hyaline cell pores on the outer surface elliptic or round, few or numerous, often in 3's where the cells meet, pores on the inner surface fewer and generally smaller; hyaline cell walls adjacent to the green cells smooth, papillose, or roughened with lines of comb fibrils or alveolate ridges; in cross section green cells entirely included with no exposure on either surface, exposed equally on both surfaces, or exposed more broadly on the inner surface. Dioicous. Capsules black when mature, spores smooth to roughened or finely papillose.

The species grouped into section *Sphagnum* can generally be recognized in the field as belonging to that section by their relatively robust aspect with turgid branches and closely overlapping leaves. Plants of some species of section *Subsecundum* have a somewhat similar aspect, but generally can be told by their bluish tinge. Plants of section *Sphagnum* can easily be distinguished microscopically by the presence of fibril bands on the stem and branch cortex, the usually broader exposure in cross section of the branch leaf green cells, and by their broadly ovate branch leaves with cucullate-concave apices that are roughened on the back due to excessive resorption.

- 1. Branch leaf green cells in cross section usually broadly elliptic to almost round with end walls on both surfaces unthickened and entirely included; hyaline cells with almost no free convexity. Plants often pinkish to red, especially in sunny habitats ...... 1. S. magellanicum
- - 2. Branch leaves in cross section with green cells more or less rectangular, end walls equally thickened and exposed, lumens narrowly elliptic to lenticular ...... 2. S. centrale
- 3. Branch leaves in cross section with green cells equilateral-triangular ...... 4

			i. b. papinosian
5. Stem	leaf hyaline cells not divided; bra	nch leaf hyaline	cell walls adjacent to
	the green cells smooth		3. S. palustre

### 1. Sphagnum magellanicum Brid., Muscol. Recent. 2(1): 24. 1798. Sphagnum medium Limpr., Bot. Centralbl. 7: 313. 1881.

Plants more or less robust, in small cushions to large hummocks, bright green, variously tinged pink, solid pink, or deep red, capitulum somewhat rounded, young branches bunched. Stem cortical cells in 3-4 layers, fibrillose (often faintly so), pores 1-2 in each cell; wood cylinder reddish to brown; stem leaves large, lingulate to long-lingulate to somewhat ligulate or spatulate; hyaline cells not divided. Branches generally in fascicles of 4-5 with 2-3 spreading branches; cortical cells mostly uniporose, weakly fibrillose; branch leaves broadly ovate, deeply concave and cucullate, strongly roughened on back at the apex (best seen in profile); hyaline cells on the outer surface with numerous elliptical pores in the cell corners and along the commissures, 4-10 per cell, on inner surface with few or no pores (rarely more than 5), mainly confined to the corners and along commissures; in cross section green cells elliptic, fully included, more or less centrally placed, end walls not thickened; hyaline cell side walls adjacent to the green cells smooth. Dioicous. Antheridial branches poorly differentiated, sometimes slightly pigmented reddish or brownish. Perichaetial leaves large, ovate, hyaline cells fibrillose and porose above, toward the base uniformly narrow, elongate and pitted. Pseudostomata numerous, scattered throughout the capsule. Spores minutely papillose, more or less 25 µm.

Illustrations. Crum & Anderson (1981), Fig. 1 A-G; Crum (1984), Fig. 1.

In small cushions to large hummocks in a variety of sun and shade habitats, poor to rich peatlands, Alder, Spruce, *Chamaedaphne*, Red Maple, Hemlock and *Thuja* swamps. In Maine known from Androscoggin (*Allen 22475* DUKE, MO), Aroostook (*Worthley 1539* DUKE, MO), Cumberland (*Allen 15936* DUKE, MO), Franklin (*Correll & Correll 11137* DUKE), Hancock (*Pedano 410* DUKE, MO), Kennebec (*Andrus 7192* DUKE), Lincoln (Allen & Pursell *Maine Mosses 5* DUKE, MAINE, MO, NY, US), Oxford (*Reed 8/25/35* DUKE), Penobscot (*Harvey 8* NY), Piscataquis (*Hermann 19152* DUKE, NY), Sagadahoc (*Allen 15753* DUKE, MO), Somerset (*Ladd 8884* MO), Waldo (*Norton 4* DUKE), Washington (*McCleary 16614* DUKE, MO), and York (*Allen 22036* DUKE, MO) Counties.

Sphagnum magellanicum is common and essentially world wide in distribution. It can usually be distinguished in the field by its characteristic pinkish to reddish color. It is the only member of section *Sphagnum* with this coloration, although in shade and sometimes even in full sun, for unknown reasons, it occasionally fails to develop a red color. Microscopically, it can be identified by examining branch leaf cross sections which reveal entirely included, typically elliptical

green cells that are not thickened at the ends. Unfortunately, S. magellanicum can sometimes have lenticular-shaped green cells in section and these collections can be difficult to distinguish from S. centrale. In general, the hyaline cells of S. magellanicum in cross section have very little convexity on either surface, while those of S. centrale have more convexity on the outer than on the inner surface.

Sphagnum compactum (section Rigida) is similar to S. magellanicum in having entirely included green cells and denticulate branch leaf margins due to the presence of resorption furrows. It differs from S. magellanicum in having stem cortical cells that lack fibrils and pores. Furthermore, although the branch leaves of S. compactum can rarely be slightly cucullate they are not as strongly cucullate as the branch leaves of S. magellanicum and never roughened on the back. In addition, in S. magellanicum the stem leaves are as long or longer than the branch leaves while in S. compactum the stem leaves are much shorter than the branch leaves. At times the fibrils on the branch cortical cells of S. magellanicum can be faint or almost lacking, and so other characters must be relied upon to identify the species.

 Sphagnum centrale C. Jens., Bih. Kongl. Svenksa. Vetensk.-Akad. Handl. 21, 3(10): 34. 1896.

Sphagnum palustre ssp. intermedium Russ., Schriften Naturf.-Ges. Univ. Dorpat 3: 28. 1887.

Sphagnum papillosum (Russ.) Warnst. var. intermedium (Russ.) Warnst., Hedwigia 30: 160. 1891.

Sphagnum palustre var. centrale (C. Jens.) Eddy in Daniels & Eddy, Handb. Eur. Sphagna 50. 1985.

Plants robust, generally in compact mats, light-green to yellowish. Stem cortical cells in 3–4 layers, weakly fibrillose, pores 1–4 in each cell; wood cylinder greenish to brownish; stem leaves lingulate, rounded at the apex; hyaline cells not divided, usually not fibrillose, generally somewhat resorbed on both surfaces. Branches in fascicles of 4–5 with 2 spreading branches; cortical cells weakly fibrillose; branch leaves broadly ovate, concave-cucullate, roughened on the back at the apex; hyaline cells on the outer surface with up to 6 elliptic, ringed pores in 2's or 3's at ends and corners, and along commissures, on the inner surface at times with 3 smaller, mildly elliptical to round pores at the cell junctions and 1–3 along the commissures; in cross section, green cells elliptic to nearly lenticular, about equally exposed on both surfaces, end walls thickened, sometimes narrowly so. Dioicous. Antheridial branches little differentiated. Pseudostomata mostly confined to the base of the capsules. Spores nearly smooth to minutely roughened, more or less 25  $\mu$ m.

Illustrations. Crum & Anderson (1981), Fig. 1 H-N; Crum (1984), Fig. 2.

In mats, shaded depressions in *Thuja* and other somewhat calcareous swamps, often temporarily submerged. In Maine known from Androscoggin (Allen & Pursell *Maine Mosses 102* DUKE, MAINE, MO, NY, US), Aroostook (*Worthley me-170* DUKE, MO), Cumberland (*Lowe 3182* MO), Franklin (Allen & Pursell *Maine Mosses 103* DUKE, MAINE, MO, NY, US), Hancock (*Bowers 10083* DUKE, MO), Oxford (*Dunham 19* DUKE), Piscataquis (*Crane 598* DUKE), Somerset (*Allen 21467A* DUKE, MO), and Washington (*Worthley me-227* DUKE, MO) Counties.

Sphagnum centrale is often confused with unusual forms of S. papillosum. Normally, S. papillosum differs from S. centrale in having the branch leaf hyaline cell walls adjacent to the green cells finely, densely papillose, and narrowly triangular green cells that are exposed only on the inner surface. In S. centrale the branch leaf hyaline cell walls are smooth and the elliptic to nearly lenticular green cells have thickened end walls that are equally exposed on both surfaces.

There are, however, forms of *S. papillosum* that have smooth branch leaf hyaline cell walls adjacent to somewhat trapezoidal green cells. These contrary forms, known as *S. papillosum* var. *laeve* Warnst., can be troublesome to identify. In distinguishing the two species it is helpful to note that the stem leaf hyaline cells of *S. papillosum* are 1-divided, except toward the base, while those of S. centrale are not divided.

Daniels & Eddy, (1985) found a resemblance between S. centrale and S. palustre in Europe and the British Isles, and as a result treated S. centrale as a variety of S. palustre. North American material of S. centrale, however, does not indicate such a close resemblance. The principal differences between these two are found in the shape and exposure of the branch leaf green cells. In North American plants of S. centrale the green cells in cross-section are rather narrowly elliptic or lenticular and exposed on both surfaces owing to a thickening of the cell ends. In Maine plants of S. palustre the green cells in cross-section are mostly narrowly isosceles-triangular (rarely trapezoidal) and exposed only on the inner surface.

3. Sphagnum palustre L., Sp. Pl. 1106. 1753.

Sphagnum palustre L. var. cymbifolium Ehrh., Hannover. Mag. 15: 235. 1780. Sphagnum cymbifolium (Ehrh.) Hedw., Fund. Hist. Nat. Musc. Frond. 2: 86. 1782. Sphagnum vulgare Michx., Fl. Bor.-Amer. 2: 285. 1803.

Plants low to robust, sometimes in extensive, shallow to deep, cushions, light yellowish green or brownish. Stem cortical cells in 3–4 layers, fibrillose, pores 2–7 in each cell; wood cylinder brown; stem leaves large, elongate-lingulate or

sometimes spatulate; hyaline cells not divided, occasionally fibrillose, generally resorbed and with one or more membrane gaps on the outer surface. Branches stout, in fascicles of 4-5, with 2 spreading branches; cortical cells often uniporose, fibrillose; branch leaves imbricate to spreading or squarrose, broadly ovate, concave-cucullate, roughened on the back at the apex; hyaline cells on the outer surface with large, rounded to elliptic, end and corner pores, often in groups of 2 or 3, pores more numerous toward the base, sometimes with individual pores enclosed in loop-like or sigmoid fibrils (i.e, ringed), sometimes with numerous elliptic or round commissural pores, one between each fibril, on the inner surface with fewer, round pores, mostly confined to the cell center; in cross section green cells isosceles-triangular, exposed only on the inner surface, rarely somewhat broadly trapezoidal with broader exposure on the inner surface; hyaline cell side walls adjacent to the green cells smooth or variously marked with a network of very faint to conspicuous ridges. Dioicous. Antheridial branches poorly differentiated, perigonial leaves sometimes slightly brownish. Perichaetial leaves elongate-ovate, hyaline cells fibrillose and porose above, toward the base cells uniformly narrow. Spores granular, more or less 25 µm.

Illustrations. Crum & Anderson (1981), Fig. 2; Crum (1984), Fig. 4.

In various wet lands, lake and pool margins, wooded swamps, poor fens, bogs, seepage cliffs, and cattail marshes in both open and shaded habitats. In Maine known from Androscoggin (*Allen 14704* DUKE, MO), Cumberland (Allen & Pursell *Maine Mosses 6* DUKE, MAINE, MO, NY, US), Hancock (*Magill 11804* DUKE, MO), Kennebec (*Gordon 16* DUKE), Lincoln (*Allen 1301* MO, NY), Oxford (*Norton 3* DUKE), Penobscot (*sin. nom. 8/20/57* DUKE), Piscataquis (*Hermann 19155* DUKE), Sagadahoc (*Allen 14593* DUKE, MO), Washington (*Pursell 12146* DUKE, MO, NY), and York (*Redfearn 33842* DUKE, MO) Counties.

Sphagnum palustre and S. papillosum are very similar in aspect, and in fact they are impossible to separate in the field. Furthermore, the branch leaves in cross section of both species have isosceles-triangular green cells that are usually exposed only on the inner surface. Normally, S. papillosum is distinguished from S. palustre by its branch leaf hyaline cells that are papillose on the side walls adjacent to the green cells. In contrast the branch leaf hyaline cells of S. palustre are smooth. There is an expression of S. papillosum (as noted above sometimes called S. papillosum var. laeve) with branch leaf hyaline cells that are smooth on the side walls adjacent to the green cells. This difficult expression of S. papillosum can be distinguished from S. palustre by examining the hyaline cells of the stem leaves; in S. palustre these cells are undivided, while at least some of those in S. papillosum are 1-2 divided. We have not seen any Maine specimens of S. henryense, a doubtful species which closely resembles S. palustre. It differs

from *S. palustre* only by sometimes having a network of very faint to conspicuous ridges on the side walls adjacent to the green cells.

4. Sphagnum papillosum Lindb., Acta Soc. Sci. Fenn. 10: 280. 1872.

S. papillosum var. sublaeve Warnst., in Röll, Flora 69: 471. 1886.

S. papillosum var. laeve Warnst., Sitzungsber. Naturf.-Ges. Univ. Jurjeff 10: 429. 1895.

Plants robust, usually in loose, sometimes extensive carpets, pale-green to brownish. Stem cortical cells in 3-4 layers, square, rectangular or multi-sided, fibrillose, fibrils thin and often faint, pores large, 1-2 (-5) in each cell, walls of innermost cortical cells adjacent to the wood cylinder fibrillose; wood cylinder greenish to brownish or black; stem leaves short- to long-lingulate; at least some hyaline cells divided, without fibrils or pores (unless hemi-isophyllous), most walls of both surfaces resorbed. Branches short and plump, in fascicles of 2-5 with 2 spreading branches; cortical cells often with a single pore at the upper end, fibrillose; branch leaves imbricate to spreading, broadly ovate, strongly concave, cucullate; hyaline cells on outer surface with 4-10 rounded or elliptic pores at ends and corners and along commissures, often 3 in adjoining corners, on the inner surface with variable numbers of smaller round pores toward the middle; in cross section green cells narrowly isosceles-triangular, sometimes with somewhat curved sides and rarely slightly trapezoidal with narrower exposure on the outer surface; hyaline cell side walls adjacent to the green cells usually finely papillose (sometimes lacking or scarce and faint). Dioicous. Antheridial branches not obvious, perichaetial leaves elongated, concave. Capsules with numerous scattered pseudostomata. Spores papillose, more or less 30 µm.

Illustrations. Crum & Anderson (1981), Fig. 3 A-J; Crum (1984), Fig. 6.

Occurring as thick carpets and large hummocks in minerotrophic and graminoid bogs, fens, and other exposed wet areas, including over rocks at higher elevations. In Maine known from Hancock (*Pedano 650* DUKE, MO), Kennebec (*Andrus 7188* DUKE), Oxford (*Correll & Correll 11155* DUKE), Piscataquis (*Merrill 2 NY*), Penobscot (*Lowe 8/20/57* DUKE), Sagadahoc (*Norton 19* DUKE), Waldo (*Norton 21* DUKE), and Washington (*Crum 9/91* MICH, MO) Counties.

Sphagnum papillosum is ordinarily easily recognized by its branch leaves that have hyaline cells with papillose side walls adjacent to the green cells. No other member of section Sphagnum in Maine has this feature. As noted above, however, there are some populations of S. papillosum that have branch leaves with smooth hyaline cell side walls, and these can be mistaken for S. centrale or

S. palustre. These two species, however, generally have undivided stem leaf hyaline cells, while at least some of the stem leaf hyaline cells in S. papillosum are divided. In the field S. papillosum can sometimes be recognized by its short, stout, blunt branches, and a characteristic golden to dark brownish color. Unfortunately, this coloration is not a consistent feature of the species and there are many collections, especially those from shaded situations, with green plants.

5. Sphagnum affine Ren. & Card., Rev. Bryol. 12: 44. 1885.

- Sphagnum imbricatum var. affine (Ren. & Card.) Warnst., Hedwigia 28: 370. 1889.
  - Sphagnum imbricatum ssp. affine (Ren. & Card.) Flatb., Kongel. Norske Vidensk. Selsk. Skr. (Trondheim) 1984(3): 180. 1984.
  - Sphagnum imbricatum var. flagellare (Röll) Card., Répert. Sphagnol. 80. 1884.

Plants moderately robust, in mats, cushions, hummocks, or carpets, pale to dark-green, yellowish to dark-brown. Stem cortical cells in 3-4 layers, square to rectangular, delicately fibrillose, pores large, 1-11 in each cell, sometimes coalesced, walls of innermost cortical cells adjacent to the wood cylinder with well-defined, cross-striate comb fibrils; wood cylinder generally black; stem leaves (often on the same plant) variable in length, lingulate, rarely slightly ligulate, with a broad, rounded apex, much resorbed, hyaline cells 1-2 divided, lacking comb fibrils. Branches usually in fascicles of 5, with 2 spreading branches; cortical cells with (0)-1-(2) pores, fibrillose; branch leaves usually somewhat spreading to sub-squarrose, ovate-cucullate, roughened on the back; hyaline cells on the outer surface with few to numerous, elliptic pores in 3's at adjacent corners and along the commissures, on the inner surface with a variable number of round pores in the cell center; in cross section green cells equilateraltriangular, occasionally slightly trapezoidal, hyaline cell side walls adjacent to the green cells with or without comb fibrils, when present often restricted to extreme basal cells, variable in prominence and extension toward the apex. Dioicous. Antheridial branches poorly differentiated, perigonial leaves sometimes slightly pigmented brown. Perichaetial leaves large, ovate, hyaline cells fibrillose and porose above, toward the base uniformly narrow. Spores almost smooth, more or less 25 µm.

Illustrations. Crum & Anderson (1981), Fig. 4 ( as S. imbricatum); Crum (1984), Fig. 7 (as S. imbricatum).

Found in a variety of wetlands, both open and shaded, from wooded swamps and wet forests to open, shrubby or grass-sedge bogs, meadows, roadside ditches, moist ledges and edges of vegetation mats on exposed rocks. In Maine known from Androscoggin (Allen 22392 DUKE, MO), Aroostook (Worthley me-200

DUKE, MO), Cumberland (Allen 15911 DUKE, MO), Hancock (Rand 7/3/1891, DUKE), Knox (Norton 4 DUKE), Oxford (Parlin 9/1939 DUKE), Sagadahoc (Andrus 7157 DUKE), Waldo (Soloman 20188 DUKE, MO), and York (Allen 21317 DUKE, MO) Counties.

Sphagnum affine until recently has generally been included within the variability of S. imbricatum sensu lato. In this broad sense S. imbricatum is a widespread species that occurs throughout most of North America, Asia, and Europe (Crum 1984, 1997). Sphagnum imbricatum has over time been broken into several segregates (see Flatberg, 1984; Andrus, 1984, 1987) and treated respectively as subspecies, varieties, or distinct species. Two of these segregates, S. affine and S. austinii, occur in Maine. Although Crum (1984, 1997) found no reason to recognize any of the segregates at any level, we recognize two of them at the species level with some reluctance. They can be sorted out rather easily by the presence in the stems of S. affine of well-defined, cross-striate comb-fibrils on the inner walls of the innermost layer of cortical cells, i.e., those next to the wood cylinder, and the absence of comb-fibrils on the stem leaf hyaline cell side walls. In S. austinii the inner walls of the innermost layer of stem cortical cells lack comb-fibrils, but the stem leaf hyaline cell side walls have well-developed comb-fibrils. Unfortunately, the outer walls of the stem cortical cells in both taxa are generally finely, delicately fibrillose, and extreme care must be exercised in removing the cortex and making sure that the inner and outer walls are distinguished. Andrus (1984, 1987) suggested that the branch cortical cells of S. austinii are connected by funnel-shaped end walls; we have not been able to confirm this observation in our material. According to Flatberg (1984) S. imbricatum sensu stricto is not known from North America and seems to be restricted to Asia. Specimens from our area named S. imbricatum are either Sphagnum affine (sensu Flatberg) or less likely S. austinii. Sphagnum austinii is rare in Maine, but abundant on the Pacific Coast of North America, south of Alaska.

6. Sphagnum austinii Sull. in Aust., Musci Appalach. [3]. 1870.

Sphagnum imbricatum ssp. austinii (Sull.) Flatberg. Kongel. Norske Vidensk. Selsk. Skr. (Trondheim) 1984(3): 46. 1984.

Sphagnum carlottae Andrus in Andrus & Vitt, Sphagnoth. Bor.-Amer. No. 189. 1982.

Plants fairly robust, in compact hummocks, reddish to yellowish brown. Stem cortical cells in 3–4 layers, square to rectangular, delicately fibrillose, pores 4–8 in each cell, walls of the innermost cortical cells adjacent to the wood cylinder without comb fibrils, at most with a few thin, widely separated fibrils; wood cylinder brown to blackish; stem leaves ligulate, almost straight-sided, to

somewhat lingulate and broadly rounded at the apex, moderately bordered with fringed resorbed cells, especially at the rounded apex, hyaline cell side walls adjacent to the green cells with comb fibrils, many of which are resorbed, leaving short stubs along the walls, hyaline cells infrequently 1-septate, usually non-septate. Branches in fascicles of 3, with 2 spreading and 1 pendent branches, fascicles generally crowded, branches tightly imbricate and pointed; cortical cells with 0–2 pores, fibrillose; branch leaves large, usually broadly ovate with cucullate apex, roughened on the back at the apex; hyaline cells on the outer surface with few to numerous, elliptic pores in 3's at adjacent corners and along the cell center; in cross section green cells equilateral-triangular with greatest exposure on the inner surface, hyaline cell side walls adjacent to the green cells with numerous and distinct comb fibrils extending almost to the apex. Sporophytes not seen from North America.

Illustrations. Andrus (1984), Figs. 3-7; Flatberg (1984), Figs. 12C-D, 13D, 18D-E.

In hummock with Sphagnum fuscum. In Maine known from Kennebec (Andrus 7198 DUKE) and Washington (Spaulding 101 DUKE, MO) Counties.

Sphagnum austinii is distinguished from S. affine principally by the absence of comb fibrils on the innermost walls of the stem cortical cells adjacent to the wood cylinder and by the presence on the stem leaves of comb fibrils on the hyaline cell side walls adjacent to the green cells. In contrast S. affine has well-defined, cross-striate comb fibrils on the innermost walls of the stem cortical cells, but the stem leaf hyaline cells lack comb fibrils. Andrus (1987) gives in table form a helpful comparison of the differences between these two species.

 Sphagnum section Rigida Lindb., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 19: 135. 1862.

Plants in low-growing, compact cushions or loose mats. Stem and branch cortical cells without fibrils; stem cortical cells without pores; branch cortical cells uniporose at upper ends, somewhat retort-like. Stem leaves very small, less than 1 mm long, lingulate to triangular; hyaline cells not divided, without pores or fibrils, unless hemi-isophyllous. Branch leaves often squarrose, longer than stem leaves, 1.5–3.0 mm long, broad, ovate to elliptical, concave, broadly truncate at the apex, not or only slightly cucullate, not roughened at the back of the apex; margins somewhat denticulate because of resorption furrows.

Members of section *Rigida* share several characters with those of section *Sphagnum*, such as branch leaves with both resorption furrows and a tendency for the hyaline cells to have pores grouped in 3's at adjacent cell angles. In section

*Rigida*, however, the branch hyaline cells have pores grouped in 3's on the inner surface while in section *Sphagnum* they are grouped in 3's on the outer surface. The two Maine species of section *Rigida* also differ from those of section *Sphagnum* in having efibrillose stem and branch cortical cells, and branch leaves with apices broadened at back but not strongly cucullate and roughened.

## 7. Sphagnum compactum DC. in Lam. & DC., Fl. Franç. 2: 443. 1805.

Plants generally short, forming dense cushions, mostly with crowded fascicles that conceal the stem, sometimes taller with fascicles farther apart. Stem cortical cells in 2–3 layers, efibrillose, outer cortical cells aporose; stem leaves small, scarcely 1 mm long, concave, lingulate to oblong-triangular, auriculate at the base, bordered in the lower half, hyaline cells not divided. Branch cortical cells in one layer, efibrillose; branch leaves larger than the stem leaves, unranked, imbricate to squarrose, involute to concave but not roughened at back above; margins with resorption furrows; hyaline cells on the outer surface with few to many rather large, rounded pores near the commissures, often with numerous pseudopores, on inner surface usually with pores grouped in 3's at adjacent cell angles; in cross section green cells slightly elliptical, entirely included, with thinwalled connections between the inner and outer cell walls. Monoicous. Spores smooth to finely papillose, more or less 30  $\mu$ m.

## Illustrations. Crum & Anderson (1981), Fig. 7 A-L; Crum (1984), Fig. 9.

In small, compact cushions on periodically wet sand, siliceous rock, and moist or wet soil in open or sometimes shaded places. In Maine known from Hancock (*Redfearn 37752* DUKE, MO), Kennebec (*Allen 14772* DUKE, MO), Knox (*Dunham 7/1939* DUKE), Lincoln (*Allen 5973* MO), Oxford (Allen & Pursell Maine Mosses 152 DUKE, MAINE, MO, NY, US), Piscataquis (*Hermann 19586* DUKE), and Washington (*Pedano 379* DUKE, MO) Counties.

Sphagnum compactum is best recognized by its compact habit, crowded fascicles, and mostly pale yellow-green to light-brown color. Only rarely is the species loosely branched. Infrequently plants of *S. compactum* can be tinged (but never entirely) pinkish red, and these pinkish plants can be confused with forms of *S. magellanicum* that have faintly fibrillose branch cortical cells. *Sphagnum compactum*, however, consistently differs from *S. magellanicum* in having branch leaves that at the apex are generally involute-concave, only very slightly cucullate, and never roughened on the back.

Although S. compactum and S. strictum are occasionally confused the two species differ in several branch leaf features. A good feature separating the two is found in the form and position of the green cells in cross section. Those of S. strictum are triangular and exposed more broadly on the outer surface, while those of S. compactum are elliptic and completely enclosed within the hyaline cells. Furthermore, in cross section the hyaline cell end walls adjacent to the green cells of S. compactum are entirely smooth, but in S. strictum they are usually finely papillose, although sometimes with only a few scattered papillae. In addition, S. compactum often has numerous pseudopores (i.e., small, pore-like structures encircled by fibril rings but not perforated) on the outer surface of the branch leaves, while those of S. strictum have few or no pseudopores.

8. Sphagnum strictum Sull., Musci Allegh. No. 201. 1845 [1846].

S. humile Schimp. in Sull., Mem. Amer. Acad. Arts, n. ser. 4: 175. 1849.

S. garberi Lesq. & James, Proc. Amer. Acad. Arts 14: 133. 1879.

Plants moderate-sized, mostly low and more or less densely branched, occasionally tall and loosely branched, yellow-green to occasionally reddish. Stem cortical cells in 1–3 layers, efibrillose, outer cortical cells aporose; stem leaves very small, less than 1.0 mm long, triangular with blunt, rounded apices, scarcely auriculate, border not well-developed at base. Branch cortical cells in one layer, efibrillose; branch leaves large, more than 2.5 mm long, ovate, sub-squarrose; margins with resorption furrows; hyaline cells on the outer surface with up to 6 non-ringed pores, with few or no pseudopores, on inner surface with 2–4 elliptic ringed pores, often in 2's or 3's at adjacent corners, hyaline cell side walls adjacent to the green cells minutely papillose with few or many papillae; in cross section green cells isosceles-triangular or trapezoidal, more broadly exposed on the outer surface. Sexuality uncertain. Spores coarsely papillose, more or less 36  $\mu$ m.

Illustrations. Crum & Anderson (1981), Fig. 7 M-S; Crum (1984), Fig. 10.

In coastal cedar swamp. In Maine known from Hancock (Faxon 6/25/1891 MO, NY) and Washington (Crum 9/1991 DUKE, MO) Counties.

Sphagnum strictum is apparently uncommon in Maine. The presence of branch leaves with a resorption furrow distinguishes S. strictum from all Maine species of Sphagnum except members of Sphagnum section Sphagnum, S. molle, and S. compactum. Members of Sphagnum section Sphagnum differ from S. strictum in having fibrillose stem and branch cortical cells and branch leaves roughened on back near the apex; S. molle differs in having branch leaf green cells in cross section more broadly exposed on the inner surface. In contrast the stem and branch cortical cells of S. strictum are efibrillose, the branch leaves are not roughened on back near the apex, and the green cells in cross section are more broadly exposed on the outer surface.

Sphagnum strictum and S. compactum are the only members of section Rigida in Maine. The species can be distinguished by examining branch leaf cross sections. In S. compactum the hyaline cell end walls adjacent to the green cells are smooth and the elliptical green cells are completely included. In contrast S. strictum has papillose hyaline cell end walls adjacent to triangular green cells that are exposed more broadly on the outer surface. Furthermore, S. compactum has numerous pseudopores on the outer surface of the branch leaves, while those of S. strictum have few or no pseudopores.

3. Sphagnum section Squarrosum (Russ.) Schimp., Syn. Musc. Eur. (ed. 2) 835. 1876.

Plants moderate-sized to robust with a conspicuous terminal bud. Stem cortical cells in 2–4 layers, efibrillose, enlarged, thin-walled, usually without pores, sometimes with a single pore or pseudopore at the upper end; stem leaves more or less flat, ovate to ovate-lingulate, with broad somewhat perforated or fringed apices; margins scantly border above and below, hyaline cells not divided. Branch cortical cells in 1–2 layers, efibrillose, of two kinds, some enlarged with retort-like upper pores, others smaller and without pores; branch leaves spreading or strongly squarrose at least when dry; hyaline cells with large, rounded to somewhat elliptic pores on both surfaces; in cross section green cells triangular or trapezoidal, more exposed on the outer surface, hyaline cell end walls adjacent to the green cells nearly always with few to many very fine papillae.

 Branch leaves abruptly narrowed from an ovate-hastate, erect base; conspicuously wide-spreading to squarrose above; stem leaves shorter (<sup>1</sup>/<sub>2</sub>-<sup>3</sup>/<sub>4</sub>) than the branch leaves; branch leaf hyaline cells with ringed pores on the inner surface and non-ringed pores on the outer surface ... 9. S. squarrosum 

### 9. Sphagnum squarrosum Crome, Samml. Deut. Laubm. 24. 1803.

Plants tall, robust, stiff, in bright, pale-green to yellow-green carpets; terminal bud large. Stem cortical cells in 2–3 layers, without fibrils or pores; stem leaves large, 1.5 to 2 mm long, more or less 1 mm wide, oblong-lingulate with broad, rounded apices, scarcely bordered; hyaline cells mostly resorbed on both surfaces. Branch cortical cells in 1–2 layers; branches long and tapering; branch leaves conspicuously wide-spreading or squarrose from an ovate-hastate, erect base, abruptly narrowed to an involute-concave, spreading acumen, toothed across the narrow tip, 2.0–2.8 mm long; hyaline cells convex on both surfaces, on the outer surface toward the apex with 1–3 round to round-elliptic, non-ringed pores at the ends and corners, at the middle and below with 10 or more large pores in 1–2 rows, on the inner surface with 4–7 large ringed pores at ends and along commissures; in cross section green cells triangular to trapezoidal, more broadly exposed on the outer surface, hyaline cell end walls adjacent to the green cells often lightly papillose. Monoicous. Spores smooth or finely papillose, more or less 25  $\mu$ m.

Illustrations. Crum & Anderson (1981), Fig. 8 A-F; Crum (1984), Fig. 12.

Found in wooded, boggy areas, especially swampy coniferous woodlands, roadside ditches lined with *Thuja* and Hemlock, stream margins, fens, and calcareous as well as non-calcareous habitats. In Maine known from Androscoggin (*Allen 21765* DUKE, MO), Aroostook (*Allen 16300* DUKE, MO), Cumberland (Norton 72 DUKE), Franklin (*Allen 22616* DUKE, MO), Hancock (Rand 9/3/1892 MO, NY), Lincoln (*Allen 20021* DUKE, MO), Oxford (*Allen 21030* DUKE, MO), Penobscot (*Vreeland 10/18/1905* NY), Piscataquis (*Hermann 19136* DUKE), Somerset (*Allen 21536* DUKE, MO), Washington (*Holmes 156* MO), and York (*Allen 23061* DUKE, MO) Counties.

Sphagnum squarrosum is a common species in Maine that is usually easy to recognize in the field by its robust habit and strongly spreading or squarrose branch leaf tips. Slender plants of *S. squarrosum* with less-spreading branch leaves than normal can be confused with *S. teres* whose branch leaves can also be somewhat wide-spreading at the tips. In *S. squarrosum* the stem leaves are considerably smaller than the branch leaves which are generally more than 2 mm long and abruptly narrowed to the acumen, while the stem leaves of *S. teres* are as long or longer than the branch leaves which are usually less than 1.5 mm long

and gradually narrowed to the acumen. In addition, the pores of the hyaline cells toward the base of the branch leaves of *S. teres* are much larger (more like leaf gaps) than those of *S. squarrosum*.

10. Sphagnum teres (Schimp.) Ångstr. in Hartman., Handb. Skand. Fl. (ed. 8) 417. 1861.

Sphagnum squarrosum Crome var. teres Schimp., Vers. Entw.-Gesch. Torfm. 64. 1858.

Plants slender to moderate-sized in yellowish or brownish, loose to dense cushions; terminal bud large. Stem cortical cells in 3–4 layers, without fibrils or pores, although sometimes with a single large pore or pseudopore (membrane thinning) in each outer cell; stem leaves more or less flat, as large or larger than branch leaves, elliptic to lingulate-spatulate, somewhat fringed around a broad rounded apex. Branch cortical cells in 1 layer; branch leaves, erect, ovate-lanceolate, gradually narrowed to an involute-concave (at time spreading) acumen, toothed across the narrow tip, 1.0–1.5 mm long; hyaline cells on the outer surface with 4–8 large, elliptic, non-ringed pores near the commissures, on the inner surface with 1–4 irregularly rounded, non-ringed pores; in cross section green cells triangular to trapezoidal, more broadly exposed on the outer surface, hyaline cell end walls adjacent to the green cells minutely papillose. Dioicous. Spores essentially smooth, more or less 25 µm.

Illustrations. Crum & Anderson (1981), Fig. 8 G–L; Crum (1984), Fig. 13; Daniels & Eddy (1985), Fig. 35.

In red maple swamps and floating mats in ponds. In Maine known from Aroostook (*Spaulding 120* DUKE, MO), Kennebec (*Andrus 7203* DUKE, NY), Oxford (*Lowe 9/9/1942* DUKE), and Piscataquis (*Crane 596* DUKE, MO) Counties.

Sphagnum teres is rare in Maine and it is said to be a calciphile, growing as a pioneer in bog mats (Crum 1984) and in rich, weakly acid to slightly basic mires (Andrus 1980); also in red maple swamps, beaver meadows, and rarely in floating mats around pond margins. It is a northern species and should be more common in Maine than the present number of Maine collections indicates. Dried specimens of *S. teres* can sometimes be difficult to distinguish from *S. squarrosum* because in that condition its leaves tend to be somewhat squarrose at the tips. Sphagnum squarrosum, however, is generally somewhat larger than *S. teres*, and its branch leaves are usually abruptly narrowed and strongly squarrose above an erect base. Furthermore, the stem leaves of *S. squarrosum* are considerably smaller than its branch leaves (in *S. teres* the stem leaves are as long

or longer than the branch leaves) and the branch leaf hyaline cells have ringed pores on the inner surface. The hyaline cells in *S. teres* are non-ringed.

The presence of single, large, well-developed pores or pseudopores on the stem cortical cells in some populations of *S. teres* combined with its apically fringed stem leaves and large terminal bud can cause confusion with *S. girgensohnii* Russ. The two species can be distinguished by examining branch leaf cross sections: in *S. girgensohnii* the green cells have greater exposure on the inner surface; in *S. teres* the greater exposure is on the outer surface.

 Section Isocladus (Lindb.) Braithw., Sphagnac. Eur. 30. 1878. Isocladus Lindb., Öfvers. Förh. Kongl. Svenska Vetensk..-Akad. 19: 133. 1862.

Section *Isocladus* has only a single species, *Sphagnum macrophyllum* Brid., that consists of two varieties, var. *macrophyllum* and var. *floridanum* Aust. The var. *macrophyllum* occurs in Newfoundland and throughout the Nova Scotian peninsula, but skips to Long Island, New York and then continues in the Gulf and Atlantic Coastal Plain to Texas and southern Arkansas with disjunctions to the Cumberland Plateau of Tennessee and Georgia. It has not been reported from Maine. We have treated it here because Maine is in the interrupted portion of its range, and so could be found there, although the intervening coast line of New England between Long Island and Nova Scotia probably has been collected as thoroughly as any area in the United States. The var. *floridanum* is more southern, ranging in the Coastal and Gulf Plain from New Jersey to Florida, and not apt to be found in Maine.

Sphagnum macrophyllum Brid. var. macrophyllum, Bryol. Univ. 1: 10. 1826.

Isocladus macrophyllus (Brid.) Lindb., Öfvers. Förh. Kongl. Svenska Vetensk..-Akad. 19: 134. 1862.

Sphagnum georgianum Schwein. ex Sull., Mem. Amer. Acad. Arts n. ser. 4: 174. 1849.

Sphagnum macrophyllum var. burinense Maass, Bryologist 70: 181. 1967.

Plants usually coarse and robust, deep-green, normally floating, submerged or temporarily stranded. Stem cortical cells 2–3 layered, without pores or fibrils; stem leaves small, less than 1 mm long, broadly triangular, rounded at the apex, scarcely bordered at base; hyaline cells not or rarely divided, without fibrils, on the outer surface without pores, on the inner surface with 1 large central pore and several round to elliptic pores, usually in a row. Branches in fascicles of 2–3 with little or no difference between spreading and pendent branches; cortical cells without pores or fibrils, rarely with an obscure apical pore, but not retort-like; branch leaves usually very long, 4–7 mm long, increasing in length toward the end of the branches, crowded in tufts, lanceolate, ovate-lanceolate to lanceolate-

ligulate, apices acute to acuminate, stiffly tubulose when dry; hyaline cells longlinear, scarcely wider than the green cells, sinuose, without fibrils, on the outer surface with a single, median row of 5–12, more or less elliptic pores, inner surface without pores; green cells in cross section I-shaped, exposed about equally on both surfaces, lumens narrowly elliptic. Dioicous. Spores smooth to finely papillose, more or less 30  $\mu$ m.

Illustrations: Crum & Anderson (1981), Fig. 9 A-F; Crum (1984), Fig. 14 a-l.

Usually completely aquatic, growing submerged or floating along the margins of fresh water, acidic lakes, ponds and permanent shallow pools. Like *Fontinalis*, it can withstand fluctuating water levels that leaves it stranded for periods of time. Not known from Maine.

Sphagnum macrophyllum is such an unusual Sphagnum species that it was at one time placed in a separate genus. The very long leaves and growth habit of S. macrophyllum make the species somewhat similar to Fontinalis, but similarity stops there. The branch leaf hyaline cells of S. macrophyllum are exceedingly long and narrow, not much wider than the green cells, they lack fibrils and have a single, median row of 5–12, evenly spaced, round to elliptic pores that extend from tip to tip. No other Sphagnum species in North America has this morphology.

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