

15. GRIMMIACEAE Arnott

Roxanne I. Hastings

Ryszard Ochyra

Plants acrocarpous or cladocarpous, small to large, usually olivaceous to blackish green, growing in rigid cushions, tufts, mats or patches. **Stems** erect, ascending, or prostrate, dichotomously to irregularly branched. **Leaves** erect and tightly appressed to crisped when dry, erect-spreading to patent when wet, lanceolate to ovate-lanceolate, less often ovate, oblong-ovate, linear, or lingulate, keeled, canaliculate, to broadly concave, smooth or sometimes longitudinally plicate, rarely with adaxial lamellae (*Indusiella*), margins plane, incurved, or variously recurved or revolute, mostly entire, 1- to multistratose, acuminate, acute to rounded-obtuse, typically with a hyaline awn, sometimes muticous, costa single, rarely spurred or forked distally (*Codriophorus* and *Niphotrichum*), usually strong, percurrent to excurrent, rarely subpercurrent, typically with one stereid band, distal lamina 1–2(–4)-stratose; basal cells quadrate to elongate, rarely oblate, straight, sinuose, or nodulose, basal juxtacostal and marginal regions usually differentiated, alar cells undifferentiated or hyaline; mid leaf cells quadrate to elongate, commonly sinuose or sinuose-nodulose, usually thick-walled. **Perichaetia** terminal on tips of stems or lateral branches; perichaetial leaves differentiated or not. **Seta** short to long, smooth or rarely papillose. **Capsule** usually erect, usually ovoid, obloid, cylindrical or cupulate, symmetric or rarely strongly ventricose at the base and gibbous, smooth or sulcate; annulus present or absent, often compound, deciduous or persistent; operculum mammillate to long-rostrate, sometimes attached to the columella after dehiscence (most *Schistidium*); peristome present, seldom rudimentary or absent, consisting of 16 teeth, lanceolate to linear, entire, perforated or cribose, variously split into 2 or 3 unequal prongs or divided nearly to the base into two filiform somewhat paired segments, smooth or variously ornamented. **Calyptra** small to large, covering only the operculum to half or more of the capsule, cucullate, mitrate, or mitrate-campanulate, smooth or plicate, naked, sometimes papillose, slightly to distinctly lacerated or deeply lobed at the base. **Spores** globose, smooth or papillose.

Genera ca. 11, species ca. 325 (9 genera, 109 species in the flora): worldwide.

Most species in the Grimmiaceae are xerophytic and colonizers of bare, usually dry and exposed rocks and stones, forming predominantly dark green to blackish cushions or tufts. However, some species occur on wet or damp rocks along watercourses and lakes or in seepage sites. They rarely inhabit soil and only a few species are epiphytes.

The Grimmiaceae is classically distinguished by quadrate to short-rectangular mid leaf cells typically sinuose to nodulose and thick-walled, and leaves usually awned, often with the awns long and toothed or papillose. There is a wide range of variation. While awns are present in most species, length varies from a short, translucent apiculus to exceeding the length of the lamina. Awns can be flat or terete, smooth or denticulate, spinose or papillose, and long-decurrent or not. Similarly, mid leaf cells range from oblate to long-rectangular and sinuose to almost straight. The range of variation in these characters makes it difficult to describe this family in simple and unequivocal terms.

The generic classification within the Grimmiaceae has long been a subject of controversy. In traditional treatments the family is considered to include the two largest genera, *Grimmia* and *Racomitrium*, with several peripheral, mostly mono- or oligotypic genera, including *Aligrimmia* R. S. Williams, *Coscinodon*, *Coscinodontella* R. S. Williams, *Indusiella*, *Jaffueliobryum*, and *Leucoperichaetium* Magill. A number of segregates have been split from the large and heterogeneous *Grimmia*, namely *Dryptodon* Bridel, *Guembelia* Hampe, *Hydrogrimmia* (I. Hagen) Loeske, *Orthogrimmia* (Schimper) Ochyra & Żarnoweic, *Schistidium*, and *Streptocolea* I. Hagen. In this treatment, only *Schistidium* is accepted. *Racomitrium* has been divided into four sharply delimited genera and the group is recognized at the subfamily level.

R. Ochyra et al. (2003) used two peristome types to divide Grimmiaceae into two subfamilies, Grimmioidae and Racomitrioidae. The *Schistidium*-type peristome defines the Grimmioidae. This peristome has lanceolate teeth that are entire or perforate and distally usually split into two or three unequal prongs that are smooth to ornamented. They have a distinctly thick and trabeculate abaxial side and a thin adaxial side. There is no basal membrane. In the *Racomitrium*-type peristome, which defines the Racomitrioidae, the teeth are linear and divided nearly to the base into two filiform branches. The teeth are equally thickened and less prominently trabeculate on both adaxial and abaxial sides. They usually arise from a low, basal membrane and often have a prostome.

SELECTED REFERENCES Churchill, S. P. 1981. A phylogenetic analysis, classification and synopsis of the genera of the Grimmiaceae (Musci). *Advances Cladist.* 1: 127–144. Jones, G. N. 1933. Grimmiaceae. In: A. J. Grout. *Moss Flora of North America, North of Mexico.* 3 vols. in 12 parts. Newfane, Vt. and New York. Vol. 2, pp. 1–60.

1. Acrocarpous; stems erect to ascending, with or without central strand; basal cells of lamina without spiral thickenings, insertion concolorous with distal cells or hyaline; costa in transverse section with 2 or occasionally with 3–6 adaxial cells near base, usually not markedly larger than abaxial cells; autoicous or dioicous; peristome teeth without basal membrane, entire or divided distally; epidermal cells of vaginula with straight walls 15a. Grimmiaceae subfam. Grimmioidae, p. 205
1. Cladocarpous or rarely acrocarpous; stems often prostrate, without central strand; basal cells of lamina often with spiral thickenings, forming a colored strip along the insertion; costa in transverse section with (2–)3–15 adaxial cells near base, much larger than abaxial cells; dioicous; peristome teeth mostly with basal membrane, cleft into 2–3 filiform branches at least to middle or irregularly divided in distal portion; epidermal cells of vaginula with sinuose-nodulose walls 15b. Grimmiaceae subfam. Racomitrioidae, p. 266

15a. GRIMMIACEAE Arnott subfam. GRIMMIOIDEAE Brotherus in H. G. A. Engler and K. Prantl, *Nat. Pflanzenfam.* 215(I,3): 444. 1902 (as Grimmiaceae)

Plants acrocarpous. **Stems** erect, central strand present or absent. **Leaves** erect or distally curved, rarely crisped, broadly oblong ovate, ovate-lanceolate, or narrowly lanceolate; margins plane, incurved or recurved, entire to occasionally denticulate distally, costa entire distally, percurrent

to excurrent, smooth, in transverse section semi-terete, occasionally terete, elliptical or reniform, with 2 or occasionally with 3–6 adaxial cells near base, usually not markedly larger than abaxial cells, often excurrent as a long awn, awn smooth to toothed but not papillose; laminal cells smooth, mammillose, or papillose; basal cells quadrate to elongate, straight to sometimes sinuous, rarely sinuose-nodulose, thin- to thick-walled, without spiral thickenings, hyaline along insertion or concolorous with more distal basal cells; mid leaf cells mainly quadrate, to short rectangular, often sinuose but not sinuose-nodulose. **Specialized asexual reproduction** absent or occasionally present as gemmae borne in axils of distal leaves or on leaf tips. **Sexual condition** autoicous or dioicous. **Seta** short to long, straight, arcuate, or sigmoid, smooth, one per perichaetium; vaginula with straight epidermal cells. **Capsule** usually erect, rarely pendent, immersed to long-exserted, symmetric to ventricose, ovoid, obloid or cylindrical, sometimes globose, smooth or distinctly striate; stomata present or absent; annulus persistent or deciduous; operculum mammillate to long-rostrate; peristome absent basal membrane, distinctly thicker and trabeculate on the abaxial side, entire or split distally. **Calyptra** cucullate, mitrate, or mitrate-campanulate, smooth or plicate, not papillose, covering operculum to entire capsule.

Genera ca. 8, species ca. 250 (5 genera, 81 species in the flora): worldwide.

Species of Grimmioidae are separated from those of the Racomitrioideae by features of the peristome, leaf cells that are straight to sinuose, and awns that are smooth to toothed. The Racomitrioideae have leaf cells that are strongly sinuose-nodulose, and awns that are sometimes smooth but are often papillose. The leaf attachments of the Racomitrioideae are brightly colored whereas those of Grimmioidae are hyaline or concolorous with the rest of the lamina (except *Grimmia leibergii* and *G. attenuata* which are yellow or orange). All Racomitrioideae have a straight or slightly arcuate seta that can be either smooth or papillose. Their capsules are smooth or almost so. In Grimmioidae the seta can be straight, arcuate, or sigmoid and are always smooth; capsules range from smooth to deeply plicate.

SELECTED REFERENCE Deguchi, H. 1979. A revision of the genera *Grimmia*, *Schistidium*, and *Coscinodon* (Musci) in Japan. J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 16: 121–256.

1. Columella usually attached to operculum and deciduous with it; calyptra small, covering only operculum, mitrate or cucullate, smooth; capsule immersed to emergent; seta straight; leaf margins plane to recurved 1. *Schistidium*, p. 207
1. Columella not attached to operculum; calyptra small to large, mitrate, cucullate or erose, smooth or plicate; capsule exserted, occasionally immersed; seta straight, sigmoid or arcuate; leaf margins plane, recurved, or incurved.
 2. Entire lamina beyond the base spirally inrolled; leaves muticous or with a hyaline apiculus of one or two cells, cucullate; known only from Alaska 5. *Indusiella*, p. 265
 2. Laminal margins beyond the base plane, recurved or incurved but never inrolled; leaves usually awned, rarely muticous, rarely cucullate; widely distributed.
 3. Calyptra less than 1/2 length of capsule, cucullate or mitrate, smooth; awns on distal leaves usually shorter than lamina; perichaetial leaves enlarged or not 2. *Grimmia*, p. 225
 3. Calyptra large, covering at least 1/2 of capsule, campanulate-mitrate, plicate; awns on distal leaves typically longer than lamina; perichaetial leaves enlarged.
 4. Stem leaves oval to ovate-lanceolate, keeled distally, plicate or not; distal lamina 1- or 2-stratose; plants olivaceous to blackish green; acidophilic 3. *Coscinodon*, p. 258
 4. Stem leaves ovate to obovate, concave or only somewhat keeled distally, not plicate; distal lamina 1-stratose; plants yellow-green to dark olivaceous; calciphilic 4. *Jaffueliobryum*, p. 262

1. SCHISTIDIUM Bruch & Schimper, Bryol. Europ. 3: 93. 1845, name conserved
 - [Greek *schistos*, split or divided, and *-idium*, diminutive, alluding to peristome]

Terry T. McIntosh

Plants (3–)10–40(–180) mm, in dense cushions to loose mats, olivaceous, green, brown, or black, often with yellow, orange, or red tones. **Leaves** ovate-lanceolate, occasionally ovate-triangular, less commonly lanceolate to linear-lanceolate or elliptical to ligulate, keeled or concave proximally, sharply keeled or nearly flat distally, margins recurved, rarely plane or incurved, distal lamina usually 1-stratose or 2-stratose in striae or patches, rarely 2-stratose, specialized laminal and marginal chlorophyllose structures absent, mucous to long-awned, sometimes ending in a fleshy, multistratose apiculus; basal cells rectangular, with straight or sinuose and thin to thick cell walls; mid leaf and distal cells quadrate, rectangular, or ovate, rarely sub-triangular, smooth or papillose, usually sinuose and thick-walled. **Gemmae** absent. **Sexual condition** autoicous, rarely dioicous; perichaetial leaves usually enlarged. **Seta** short, straight. **Capsule** erect, immersed, symmetric, cylindrical or campanulate; annulus rudimentary or absent; operculum rostrate or rarely mamillate, usually falling attached to columella (except *S. trichodon*). **Calyptra** cucullate or mitrate, not erose, not fully covering operculum, smooth.

Species ca. 120 (30 in the flora): North America, Mexico, Central America, South America, Eurasia, Africa, Atlantic Islands, Pacific Islands, Australia, Antarctica.

The genus *Schistidium* has consistently fascinated yet confounded bryologists across North America. Treatments vary from region to region, and names applied to specimens at both the species and varietal levels have been as inconsistent as the characters used to differentiate the taxa. The treatment of the *S. apocarpum* complex by H. H. Blom (1996) and a survey of Nordic species of *Schistidium* (Blom 1998) assist in a better understanding of the taxonomy of this complex genus in North America, but many problems of taxonomic interpretation remain. Although *Schistidium* offers a great number of both gametophytic and sporophytic characters for study, some traits are not well understood and further detailed field and laboratory research is needed.

This treatment follows H. Deguchi (1979) and H. H. Blom (1996, 1998), with reservations. For example, North American specimens identified as *Schistidium recurvum* H. H. Blom seem to differ from the type in significant character states (Blom, pers. comm.), so this species has been omitted. *Schistidium lancifolium* H. H. Blom and *S. umbrosum* (J. E. Zetterstedt) H. H. Blom have been included within *S. apocarpum*. Although *S. ambiguum* Sullivant has been reported from North America and may be present, all of the North American collections named *S. ambiguum* that were examined have proved to be another species.

When examining a specimen of *Schistidium* certain steps are helpful. It is important to examine the leaves proximal to the perichaetial region. Transverse-sections from the distal region to mid leaf of multiple leaves are also critical in most cases. The necessity of numerous transverse-sections is apparent when studying *S. papillosum* or *S. boreale*, for example, as some leaves can be slightly papillose and unless numerous sections are made the papillae may be missed. Mature, empty capsules that are not overly degraded, although not always available, should be used. Transverse-sections of the capsules assist in the easier examination of the exothecial cells and peristome teeth. It is also useful to examine more than one capsule if available, as there can be some variation in exothecial cell makeup. As H. H. Blom (1996) pointed out, mixed

populations are present in some sites, especially in more humid areas, so care must be taken to ensure that all species in a collection are separated. Blom also provided a great amount of supplementary detail about many of the species treated here.

SELECTED REFERENCES Allen, B. 2005. Maine Mosses: Sphagnaceae–Timmiaceae. Mem. New York Bot. Gard. 91. Blom, H. H. 1996. A revision of the *Schistidium apocarpum* complex in Norway and Sweden. Bryophyt. Biblioth. 49. Blom, H. H. 1998. *Schistidium*. In: E. Nyholm. 1986+. Illustrated Flora of Nordic Mosses. 4+ fasc. Lund. Fasc. 4, pp. 287–331. Bremer, B. 1980. A taxonomic revision of *Schistidium* (Grimmiaceae, Bryophyta) 1. ...2. Lindbergia 6: 1–16, 89–117. Bremer, B. 1981. A taxonomic revision of *Schistidium* (Grimmiaceae, Bryophyta) 3. Lindbergia 7: 73–90.

1. Leaf costa with one to two well-developed stereid bands; restricted to coastal areas, often within or near the spray zone 20. *Schistidium maritimum*
1. Leaf costa stereid bands absent; sometimes found in coastal areas, but rarely within or near the spray zone.
 2. Plants usually in extensive open tufts or mats over soil, litter, and amongst plant bases in arctic fens and tundra, often along drainage channels 18. *Schistidium holmenianum*
 2. Plants usually on rock.
 3. Costa excurrent as a fleshy, multistratose apiculus, rarely tipped with a tiny denticulate awn.
 4. Leaves ovate-lanceolate, mostly erect or erect-incurved when dry, keeled throughout; fleshy apiculus short and indistinct; dioicous, sporophytes rare 9. *Schistidium crassithecium*
 4. Leaves linear-lanceolate to ovate-lanceolate, usually curved to falcate, or falcate-secund when dry, weakly keeled distally or concave throughout; fleshy apiculus prominent on most leaves; autoicous, sporophytes common.
 5. Lamina mostly 2-stratose distally, with 2-stratose strips extending to the leaf base adjacent to the costa 6. *Schistidium cinclidodonteum*
 5. Lamina mostly 1-stratose 21. *Schistidium occidentale*
 3. Costa sub-percurrent or excurrent as an awn, never as a fleshy, multistratose apiculus.
 6. Dioicous, sporophytes rare; leaves erect and usually imbricate when dry; distal lamina evenly to irregularly 2-stratose; long awns present on most leaves; plants usually fragile, with individual stems easily separated.
 7. Leaves usually ovate-lanceolate, mostly greater than 1.5 mm; distal lamina evenly 2-stratose; margins plane to incurved, awns usually straight 17. *Schistidium heterophyllum*
 7. Leaves usually ovate-triangular, mostly less than 1.5 mm; distal lamina unevenly 2-stratose; margins recurved; awns usually flexuose 28. *Schistidium tenerum*
 6. Autoicous, sporophytes usually present; leaves often curved and somewhat spreading, occasionally imbricate when dry; distal lamina 1- or 2-stratose; awns present or absent; plants not fragile.
 8. Distal laminal cells papillose, mainly on abaxial surface.
 9. Awns coarsely spinulose, often strongly decurrent; laminal cells usually strongly papillose with tall, thick papillae often on both abaxial and adaxial surfaces; Arctic species 15. *Schistidium frivollianum*
 9. Awns finely and distantly spinulose or nearly smooth, weakly decurrent or non-decurrent; laminal cells weakly papillose with short papillae mainly on abaxial surface; widespread or more southern species.
 10. Plants usually red-brown (rusty), rarely black or olivaceous; leaves ± imbricate proximal to the stem apex when dry; capsule usually cupulate 26. *Schistidium strictum*
 10. Plants olivaceous, sometimes partially reddish brown or dull black; leaves not imbricate proximal to the apex when dry; capsule usually cylindrical.

11. Plants usually dull black, usually purplish when wet; leaf cells with reddish or orange walls; capsule narrowed towards the mouth 5. *Schistidium boreale*
11. Plants usually olivaceous, sometimes with reddish tones, rarely nearly black, not purplish when wet; leaf cells with hyaline walls; capsule rarely contracted towards the mouth 22. *Schistidium papillosum*
- [8. Shifted to left margin.—Ed.]
8. Distal laminal cells smooth (note: distal abaxial costal cells and leaf margins near awn sometimes papillose).
12. Plants usually along water courses and lakes, often submerged or in splash zones, sometimes along seasonally irrigated ledges or cliffs; costa usually sub-percurrent or percurrent, sometimes excurrent as a hyaline cell, awns rare; capsule often campanulate; spores large, usually greater than 15 μm .
13. Leaves linear-lanceolate to ligulate, usually nearly flat distally; margins plane or weakly recurved, usually 1-stratose, smooth or weakly crenulate at apex . . . 1. *Schistidium agassizii*
13. Leaves ovate-lanceolate to ovate-triangular, keeled distally; margins recurved to revolute, usually 2-stratose, denticulate or smooth distally.
14. Capsule often campanulate, never narrowed towards the mouth; stems often greater than 5 mm; leaves 1.2–3.2 mm 24. *Schistidium rivulare*
14. Capsule short-cylindric or ovoid, never campanulate, usually slightly narrowed towards the mouth; stems rarely greater than 2 mm; leaves 1.2–2.2 mm 27. *Schistidium subjulaceum* (in part)
12. Plants usually in drier habitats; costa percurrent or excurrent as an awn; capsule cylindric or cupulate, rarely campanulate; spores small, usually less than 15 μm .
15. Leaves ovate-ligulate to ovate-lanceolate, often with rounded apices, mostly less than 0.7 mm; awns usually absent; capsule short, usually less than 0.6 mm 3. *Schistidium atrichum*
15. Leaves mostly ovate-lanceolate, apices usually acute, usually greater than 1 mm; awns present in most species, sometimes absent; capsule usually greater than 0.7 mm.
16. Peristome absent, rudimentary, or very short (less than 100 μm).
17. Leaves partially or completely 2-stratose distally; leaves moderately keeled distally; found only on calcareous rock 4. *Schistidium atrofuscum*
17. Leaf lamina 1-stratose, rarely with a few 2-stratose striae; leaves strongly keeled distally; not restricted to calcareous rock.
18. Capsule usually campanulate; operculum rostrate; arctic species 10. *Schistidium cryptocarpum*
18. Capsule cupulate; operculum mamillate; central North American species 12. *Schistidium flaccidum*
16. Peristome well-developed (greater than 200 μm).
19. Peristome teeth long, to 700 μm , sometimes forming a dome; columella persistent in capsule, not falling with operculum 29. *Schistidium trichodon*
19. Peristome teeth usually much shorter, never forming a dome; columella falling with operculum.
20. Plants small, often forming flattish cushions or tufts; awns very short to absent; capsule less than 1 mm, if taller then distinctly striate (*S. dupretii*).
21. Basal marginal cells often elongate-rectangular; some central basal cells usually much lighter than adjacent cells, often hyaline; exothecial cells mostly oblate or isodiametric 14. *Schistidium frigidum* (in part)
21. Basal marginal cells quadrate or short-rectangular; basal cells evenly colored; many exothecial cells elongate.

22. Capsule ovoid or cupulate, rarely campanulate, rarely striate; basal marginal cells quadrate or short-rectangular, transverse walls usually thicker than longitudinal walls; plants compact, usually olivaceous. 7. *Schistidium confertum*
22. Capsule short-cylindrical, usually finely striate when empty; most basal marginal cells oblate, cell walls evenly thickened; plants open, usually brownish 11. *Schistidium dupretii*
- [20. Shifted to left margin.—Ed.]
20. Plants small to large, usually forming rounded cushions, tufts, or mats; awns well developed, occasionally absent; capsules usually greater than 1 mm.
23. The majority of exothecial cells of capsule wall elongate, sometimes mixed with isodiametric and, rarely, oblate cells.
24. Leaves ovate-triangular, occasionally ovate-lanceolate, mostly well under 1.7 mm.
25. Distal lamina 1-stratose, occasionally with 2-stratose striae or patches; awns usually absent; capsule light (yellow-) brown, usually narrowed towards the mouth 27. *Schistidium subjulaceum* (in part)
25. Distal lamina with 2-stratose patches or 2-stratose; awns usually present; capsule red-brown, not narrowed towards the mouth 30. *Schistidium venetum*
24. Leaves ovate-lanceolate, mostly greater than 2 mm.
26. Leaf margins recurved to well below apex; distal lamina with 2-stratose patches or occasionally 2-stratose; distal laminal cells mostly rounded or short-rectangular, weakly sinuose; basal marginal cells longitudinally short-rectangular or quadrate 8. *Schistidium crassipilum*
26. Leaf margins recurved to near apex; distal lamina 1-stratose, rarely with 2-stratose striae; distal laminal cells mostly short-rectangular, strongly sinuose; many basal marginal cells oblate 25. *Schistidium robustum*
23. The majority of exothecial cells more or less isodiametric, often mixed with oblate cells, elongate cells few or absent.
27. Capsule 0.4–0.8 mm; awns long, spinulose-denticulate; basal marginal cells with transverse walls thicker than longitudinal walls 19. *Schistidium liliputanum*
27. Capsule usually 0.8 mm to 1.3 mm; awns short to long, weakly spinulose or nearly smooth; transverse basal marginal cells walls same thickness as longitudinal walls.
28. Leaves small, most well under 2 mm; costa smooth; some basal marginal cells elongate-rectangular; some basal cells usually much lighter than adjacent cells, often hyaline 14. *Schistidium frigidum* (in part)
28. Leaves larger, usually greater than 2 mm; distal abaxial costa sometimes papillose; basal marginal cells quadrate or short-rectangular; basal cells the same color.
29. Distal leaf cells 11–14 μm wide; spores 15–21 μm ; Arctic 16. *Schistidium grandirete*
29. Distal leaf cells 8–10 μm wide; spores 11–15 μm , rarely larger; widespread.
30. Awns bright white, usually strongly decurrent; distal laminal cells variable in shape and size, strongly trigonous, often guttulate, occasionally, with stellate lumina, especially at mid leaf 23. *Schistidium pulchrum*
30. Awns dull and hyaline, strongly or non-decurrent; distal laminal cells more-or-less even in size and shape, trigones weak or absent, not guttulate or stellate.
31. Leaves ovate-lanceolate, erect or curved, rarely (falcate-)secund when dry, often greater than 2.4 mm; distal leaf margins usually denticulate; abaxial surface of costa usually papillose 2. *Schistidium apocarpum*
31. Leaves narrowly ovate-lanceolate, usually curved, often falcate-secund when dry, less than 2.4 mm; distal leaf margins and costa smooth 13. *Schistidium flexipile*

1. *Schistidium agassizii* Sullivant & Lesquereux, Musc. Hepat. U.S., 104. 1856



Grimmia agassizii (Sullivant & Lesquereux) Jaeger & Sauerbeck;
G. alpicola Hedwig

Plants in open, rarely compact tufts or mats, dark olivaceous, sometimes brownish or black. **Stems** (0.9–)1.3–2.5(–5) cm, central strand absent or indistinct.

Leaves erect or curved, often toward stem, sometimes contorted when dry, linear-lanceolate to ligulate, sometimes oblong-lanceolate, weakly keeled or concave proximally, usually nearly flat distally, sometimes concave or rarely weakly keeled, 1–3.5 mm, 1-stratose; margins plane or weakly recurved proximally, plane, rarely incurved distally, smooth or weakly crenulate, sometimes eroded distally, usually 1-stratose, occasionally partly 2-stratose; apices obtuse or acute, sometimes ending in a hyaline cell; costa subpercurrent or percurrent, awn absent, smooth; basal marginal cells short-rectangular or quadrate; distal laminal cells quadrate or short-rectangular, often rounded, (7–)9–12 μ m wide, smooth, weakly sinuose. **Sexual condition** autoicous. **Capsule** light brown, rarely almost black, campanulate, rarely cupulate, 0.8–1.2 (–1.5) mm; exothecial cells isodiametric or slightly elongate, often round or irregularly angular, walls thick, often somewhat curved, trigonous; rim darker than capsule wall, sometimes red; stomata absent; peristome squarrose to revolute, 350–570 μ m, red or orange-red, finely papillose, moderately to strongly perforated. **Spores** 10–18(–25) μ m, smooth or granulose.

Capsules mature late spring to early summer. Wet or dry rocks in or along water courses and lakes; low to high elevations (0–3600 m); Greenland; Alta., B.C., N.B., N.S., Ont., Yukon; Alaska, Calif., Colo., Idaho, Maine, Md., Mass., Mich., Minn., Mont., N.Y., Oreg., Utah, Wash., Wyo.; Eurasia.

Schistidium agassizii is sometimes confused with *S. rivulare*, another dark species found along watercourses. It differs in having linear-lanceolate, almost straight-sided, and distally nearly flat leaves, with plane or weakly recurved margins. The leaves of *S. rivulare* are often lighter in color, ovate-lanceolate to ovate-triangular, and always distally keeled with recurved margins. Also, *S. rivulare* usually forms much larger patches than does *S. agassizii*. New leaves of *S. agassizii* are often yellow-green or brownish, somewhat concave-keeled distally, and are somewhat julaceous, forming finger-like projections at the tips of stems. *Schistidium subjulaceum* is another similar species that grows along watercourses but is

distinguished from *S. agassizii* by the same vegetative characters that separate the latter from *S. rivulare*, as well as by its smaller, often lighter colored, and short-cylindrical or ovoid capsules.

2. *Schistidium apocarpum* (Hedwig) Bruch & Schimper, Bryol. Europ. 3: 99. 1845



Grimmia apocarpha Hedwig, Sp.

Musc. Frond., 76. 1801;

Schistidium lancifolium H. H. Blom;

S. umbrosum (J. E. Zetterstedt)

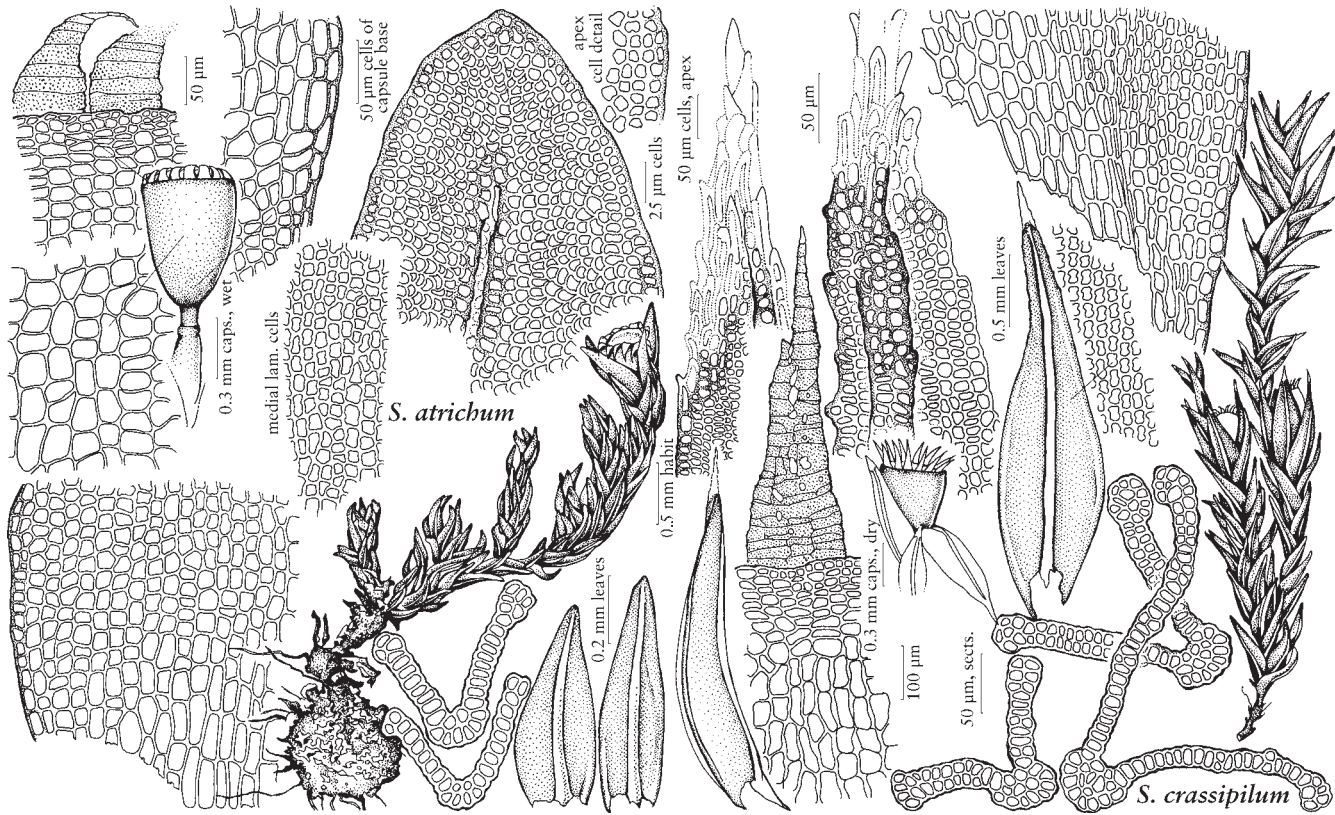
H. H. Blom

Plants in open tufts or mats, olivaceous to brownish (black), sometimes with yellowish tones.

Stems 1.2–12 cm, central strand weak or absent. **Leaves** erect or curved, rarely (falcate-) secund when dry, ovate-lanceolate, sharply keeled distally, (1.3–)1.7–2.5(–3.2) mm, 1-stratose or rarely 2-stratose in striae distally; margins usually recurved throughout or to just before the apex, usually denticulate distally, 1 or 2-stratose; apices acute or sub-obtuse; costa percurrent or excurrent as a smooth or weakly denticulate, occasionally decurrent awn, abaxial surface often papillose; basal marginal cells usually quadrate; distal laminal cells mostly short-rectangular, 8–10 μ m wide, smooth, sinuose. **Sexual condition** autoicous. **Capsule** dark red or brown, short-cylindric, 0.7–1.3 mm; exothecial cells usually quadrate, sometimes mixed with short-elongate or oblate cells, thin-walled, usually trigonous; stomata present; peristome patent or erect, often twisted, 350–600(–700) μ m, red, densely papillose, usually perforated. **Spores** 11–14(–19) μ m, granulose or smooth.

Capsules mature late spring to early summer. Rocks in somewhat shaded habitats; low to moderate elevations (0–1500 m); Greenland; Alta., B.C., N.B., Nfld. and Labr. (Nfld.), N.S., Ont., Que.; Alaska, Mich., N.Y., Vt., Wash., Wis.; Eurasia.

Although H. H. Blom (1996) considered *Schistidium apocarpum* to be restricted in the flora area to the eastern portions of North America, it is more widespread and scattered across the continent. The denticulate leaf margins, papillose abaxial costal surface, short-cylindrical capsules, and the thin-walled, often evenly quadrate exothecial cells are distinguishing characters. The long peristome teeth are also useful in identifying *S. apocarpum*. In good condition the peristome can only be confused with that of *S. trichodon*, which differs in the darker, often black color of its plants, the peristome teeth often forming a dome, and the cylindrical capsules that retain the columella.



SCHISTIDIUM

3. *Schistidium atrichum* (Müller Hal. & Kindberg)

W. A. Weber, Phytologia 33: 106. 1976 [E] [F]



Grimmia atricha Müller Hal. & Kindberg in J. Macoun and N. C. Kindberg, Cat. Canad. Pl., Musci, 65. 1892

Plants in compact, often flat cushions or tufts, olivaceous, brown, or black. **Stems** 0.3–0.8 (–1.5) cm, central strand absent.

Leaves erect, often curved towards stem when dry, ovate-ligulate to ovate-lanceolate, usually concave proximally, moderately keeled distally, 0.4–0.7 (–0.8) mm, 1-stratose, sometimes with a few 2-stratose striae distally; margins plane or recurved to just before the apex, smooth, 1-stratose or 2-stratose, rarely 3-stratose; apices rounded or sub-acute; costa sub-percurrent or percurrent, rarely excurrent as a tiny, weakly papillose awn, smooth; basal marginal cells quadrate or short-rectangular; distal laminal cells ovate or short-rectangular, 7–9 µm wide, smooth, sinuose.

Sexual condition autoicous. **Capsule** dark red-brown or light brown, short-cylindric or cupulate, rarely slightly wider at the mouth, 0.4–0.6 (–0.8) mm, occasionally finely ribbed when dry; exothecial cells of various shapes, mainly elongate or isodiametric, walls thin or unevenly thickened, straight or curved, sometimes trigonous; stomata absent; peristome erect or patent, 100–200 µm, red-brown or red, papillose, weakly perforated. **Spores** 8–11 µm, smooth.

Capsules mature late spring to early summer. Dry, often shaded mainly limestone rocks; usually high elevations; Alta., B.C.; Alaska, Calif., Colo., Idaho, Mont., Oreg., Utah, Wash.

Schistidium atrichum is the smallest North American species in the genus. Along with the small size of its leaves, stems, and capsules, the usual lack of awns on vegetative leaves and its habit of forming small, often flat cushions help to distinguish it. S. Flowers (1973) noted strong similarities between *S. atrichum* and *S. dupretii*, but the larger size and the consistently ribbed capsules separate *S. dupretii*.

4. *Schistidium atrofuscum* (Schimper) Limpricht,
Laubm. Deutschl. 1: 713. 1889



Grimmia atrofusca Schimper, Syn.
Musc. Eur. ed. 2, 240. 1876

Plants in compact cushions or tufts, dark brown(-olivaceous) or near black. **Stems** 0.6–2.5 cm, central strand distinct. **Leaves** usually erect, occasionally slightly curved, sometimes towards stem when dry, ovate-triangular to

ovate-lanceolate, moderately keeled distally, 1.2–2.1 mm, with 2-stratose patches or striae or 2-stratose distally; margins weakly recurved to just before the apex, distal half often plane, proximally often more broadly recurved on one side of leaf, 2- or 3-stratose; apices obtuse or subacute; costa sub-percurrent or percurrent, rarely excurrent as a tiny awn, smooth; basal marginal cells quadrate with transverse walls sometimes thicker than longitudinal walls; distal laminal cells usually rounded or short-rectangular, 6–9 μm wide, smooth, weakly sinuose. **Sexual condition** autoicous. **Capsule** orange- or red-brown, often yellowish, short cylindrical or cupulate, 0.75–1 mm; exothecial cells primarily elongate mixed with patches of irregularly angular isodiametric cells, walls sometimes unevenly thickened and curved; stomata absent; peristome patent, very short, 30–100 μm , or rudimentary, orange or orange-red, densely papillose, strongly perforated and unevenly margined. **Spores** 11–15(–19) μm , granulose or smooth.

Capsules mature late spring to early summer. Open to somewhat shaded limestone; moderate to high elevations (1500–2300 m); Alta., N.Mex.; Eurasia.

Schistidium atrofuscum may be the rarest North American species of the genus. It is characterized by its dark brown or nearly black, compact cushions or tufts, mostly erect, moderately keeled leaves, often 2-stratose distal lamina, and the short or rudimentary, strongly perforated peristome. G. N. Jones (1933) listed this species from Tennessee, but that has not been confirmed.

5. *Schistidium boreale* Poelt, Svensk Bot. Tidskr. 47:
256, fig. 1b, e. 1953



Plants in open tufts or mats, dull black, often yellowish green distally, usually purplish when wet, especially in older portions of stems. **Stems** 1.5–10 cm, central strand absent or indistinct. **Leaves** erect proximally, usually slightly curved distally, rarely somewhat secund when dry, ovate-lanceolate,

sharply keeled distally, 1.6–2.5 mm, 1-stratose; margins usually recurved throughout, denticulate distally, 1- or 2-stratose; apices acute; costa percurrent or excurrent as a denticulate, occasionally weakly decurrent awn, abaxial surface papillose; basal marginal cells quadrate or oblate, often trigonous; distal laminal cells mostly short-rectangular or quadrate, 8–10 μm wide, papillose, strongly sinuose with reddish or orange walls. **Sexual condition** autoicous. **Capsule** red-brown, sometimes orange-brown, ovoid-cylindric, narrowed to the mouth, 0.7–1.25 mm, rarely striate when old; exothecial cells mostly isodiametric, mainly more or less quadrate, usually mixed with a few short-elongate or oblate cells, thin-walled, with small trigones; stomata present; peristome patent or erect, dark-red or red, 190–380 μm , densely papillose, entire or slightly perforated. **Spores** 10–14 μm , granulose.

Capsules mature late spring to early summer. Somewhat shaded granite or limestone ledges; low to high elevations (0–2000 m); Alta., B.C., N.W.T., Ont., Que., Sask.; Alaska, Colo.; Eurasia.

Schistidium boreale is one of the five species of the genus in North America with papillose distal laminal cells. The combination of its dull black color, usually turning purplish when wet, reddish or orange laminal cell walls, and ovoid-cylindrical capsules that are narrowed at the mouth separates this species from the other papillose taxa. *Schistidium papillosum* is usually olivaceous and lacks colored cell walls; *S. strictum* is usually a dull red-brown, has cupulate capsules, and appears to be restricted to northwestern, coastal areas, and *S. frisvollianum*, an arctic species, is more strongly ornamented. None of these three taxa turns purple when wet. *Schistidium maritimum* occasionally has papillose distal laminal cells. That species, however, is restricted to coastal areas, its leaves are ovate-lanceolate to linear-lanceolate with 2-stratose distal laminae, and its costa has one or two well-developed stereid bands, which are absent in all other North American species of the genus.