

SCHISTIDIUM • GRIMMIA

28. *Schistidium tenerum* (J. E. Zetterstedt) Nyholm, Ill.
Moss. Fl. Fennoscand., Musci, 775. 1969



Grimmia tenera J. E. Zetterstedt,
Kongl. Svenska Vetensk. Acad.
Handl., n. s. 13(13): 17. 1876

Plants in densely compact, usually fragile (individual stems easily separated) cushions or mats, olivaceous, brownish green, or nearly black. Stems 0.5–2(–4) cm, central strand distinct. Leaves

erect, usually imbricate when dry, ovate-triangular to ovate-lanceolate, keeled distally, concave proximally, (0.7)–0.9–1.5(–1.8) mm, usually unevenly 2-stratose distally; margins usually recurved, smooth, 1-stratose or 2-stratose; apices acute; costa usually long-excurrent as a spinulose-denticulate, usually decurrent, often flexuose awn, smooth; basal marginal cells quadrate or oblate, sometimes with transverse walls thicker than longitudinal walls, trigonous; distal laminal cells quadrate, ovate, or short-rectangular, 5–8 µm wide, smooth, weakly sinuose or straight. Sexual condition dioicous. Capsule dark reddish or orange-brown, cupulate or short-cylindric,

0.6–1.1 mm; exothecial cells isodiametric or elongate, usually thin-walled; stomata present; peristome patent to squarrose, 300–420 µm, orange or light brown, papillose, strongly perforated. Spores 10–14 µm, verruculose.

Capsules mature late spring to early summer. Exposed to semi-shaded rock, often forms rather extensive patches, especially in and along rock crevices; low to high elevations (0–4500 m); Greenland; Alta., B.C., Man., N.W.T., Nunavut, Sask., Yukon; Alaska, Colo., Mont., Wash., Wyo.; Eurasia.

The densely compact mats or cushions comprised of thin, wiry stems that readily separate once disturbed characterize *Schistidium tenerum*. The usually unevenly 2-stratose, ovate-triangular, small laminae tipped with long, often flexuose, spinulose-denticulate awns distinguish it from other species of the genus and similar species of *Grimmia*. This species is closely related to the larger *S. heterophyllum*, and differences between the two are discussed under that species. Probably because *S. tenerum* is usually sterile, many collections of it remain unidentified in collections, or identified as an undetermined species of *Grimmia*.

29. *Schistidium trichodon* (Bridel) Poelt, Svensk Bot. Tidskr. 47: 253. 1953



Grimmia trichodon Bridel, Bryol. Univ. 1: 171. 1826

Plants in open tufts or extensive mats, black, dark olivaceous, or brownish-olivaceous. **Stems** 1.8–12 cm, central strand weak or absent. **Leaves** usually somewhat curved, rarely secund, ovate-lanceolate, sharply keeled distally,

1.7–2.7 mm, 1-stratose; margins usually recurved throughout and denticulate distally, 1-stratose or 2-stratose; apices acute; costa percurrent or excurrent as a short, denticulate, weakly decurrent awn, abaxial surface usually weakly papillose; basal marginal cells quadrate or short-rectangular, sometimes trigonous; distal laminal cells mostly short-rectangular, 8–10 μ m wide, usually trigonous, sinuose. **Sexual condition** autoicous. **Capsule** red-brown, cylindrical to short-cylindrical, rarely cupulate, 0.7–1.2 mm, sometimes ribbed when dry; columella persistent within capsule; exothecial cells mainly isodiametric, sometimes mixed with short-elongate cells, thin-walled, trigonous; stomata present; peristome erect or ascending, often twisted inwards and overlapping distally, forming a dome, 400–700 μ m, red, finely papillose, rarely with a few narrow slits. **Spores** 9–13 (–19) μ m, granulose or nearly smooth.

Capsules mature late spring to early summer. Usually on calcareous rock (collected once on acidic rock in Washington State), open to shaded habitats; low to high elevations (0–3500 m); B.C., N.B., Nfld. and Labr. (Nfld.), N.W.T., N.S., Que., Yukon; Alaska, Colo., Mont., Wash.; Eurasia.

The habitat, almost always on calcareous rock, its black or dark olivaceous color, the lack of long awns, the long, often domed peristome, and the persistence of the columella within the capsule make *Schistidium trichodon* a distinctive species.

30. *Schistidium venetum* H. H. Blom, Bryophyt. Biblioth. 49: 192, fig. 76. 1996



Plants in small or sometimes extensive tufts, olivaceous, often with a yellowish or brownish tinge. **Stems** 1–3.8 cm, central strand distinct. **Leaves** erect or curved, usually imbricate, ovate-lanceolate to ovate-triangular, broadly keeled distally, 1.2–1.7 (–2) mm, 1-stratose with 2-

stratose patches or evenly 2-stratose distally; margins recurved to near apex, smooth, usually 2-stratose, occasionally multistratose; apices acute or blunt; costa sub-percurrent or excurrent as a lightly denticulate, usually broad-based, and flexuose awn that often embraces a portion of the leaf apex, smooth; basal marginal cells quadrate or short-rectangular; distal laminal cells ovate or short-rectangular, 6–10 μ m wide, sinuose, trigonous. **Sexual condition** autoicous. **Capsule** red- or orange-brown, short-cylindrical, 0.8–1.1 (–1.3) mm; exothecial cells mostly elongate, mixed with isodiametric and a few oblate cells, thin-walled, sometimes trigonous; stomata present; peristome patent to recurved, sometimes twisted, 270–440 μ m, bright red or orange, densely papillose, strongly perforated with uneven margins. **Spores** 8–12 μ m, granulose or nearly smooth.

Capsules mature late spring to early summer. Wet ground of arctic fens, tundra, and drainage channels; low elevations (0–100 m); Greenland; B.C., N.W.T., Nunavut, Que.; Wash.; Europe.

Schistidium venetum is a distinctive, rather small species characterized by patchy or completely 2-stratose distal laminae, a lightly denticulate and usually broad-based awn that frequently embraces the upper portions of the lamina, and strongly perforated, uneven-sided peristome teeth.

2. GRIMMIA Hedwig, Sp. Musc. Frond., 75. 1801 • [For J. F. K. Grimm, 1737–1821, physician and botanist of Gotha, Germany]

Roxanne I. Hastings

Henk C. Greven

Drytodon Bridel; *Hydrogrimmia* (I. Hagen) Loeske

Plants 5–40 (–70) mm, in dense cushions to loose mats, olivaceous, dark black-green to rusty-red-brown. **Leaves** broadly oblong-ovate, oblong-lanceolate, to narrowly ovate-lanceolate, rarely ligulate, concave or keeled distally, margins plane, incurved or recurved, distal lamina 1-stratose

to multistratose, specialized laminal and marginal chlorophyllose structures absent, muticous to long-awned but awns only rarely longer than lamina; basal cells oblate to elongate, with straight or sinuose and thin to thick cell walls; mid leaf and distal cells quadrate to rectangular, usually sinuose and thick-walled. **Gemmae** present or absent. **Sexual condition** autoicous or dioicous; perichaetial leaves enlarged or not. **Seta** short to long, straight, arcuate, or rarely sigmoid. **Capsule** erect, rarely pendent, immersed to long exserted, symmetric or rarely ventricose (*Gasterogrimmia*), ovoid to obloid, rarely globose or cylindrical; annulus poorly differentiated or well-defined comprised of quadrate, thin-walled or quadrate to rectangular, thick-walled cells; operculum mammillate, conic, or rostrate, falling detached from the columella. **Calyptra** mitrate or cucullate, not erose, small to medium, usually covering $\frac{1}{2}$ or less of capsule, sometimes just covering operculum, smooth.

Species 95 (43 in the flora): North America, Mexico, Central America, South America, Eurasia, Africa, Pacific Islands, Australia, Antarctic.

The genus *Grimmia* is found on all continents. However, nearly half (44) of the species are endemics and have restricted distributions. Most species of *Grimmia* prefer dry and temperate or cold environments—there is no species only known from tropical areas. Nearly all species of *Grimmia* are saxicolous with a marked preference for acidic bedrock. Only the subgenus *Gasterogrimmia* prefers calcareous rock, with a few other species in other subgenera characteristic of neutral to basic substrates.

Hastings has attempted to place species in the subgenera *Gasterogrimmia*, *Guembelia*, and *Litoneuron* into groups of related or similar-looking ones. Because of the diversity within subg. *Rhabdogrimmia*, Greven felt it most convenient to present this group largely in alphabetical order. While the proper subdivision of *Grimmia* remains uncertain, both authors agree that for purposes of identification, the present division is best for this very complicated genus. Hastings authored the accounts for species 1–8, 10, 11, 13–16, 18, and 20–24, Greven those for species 10, 13, 18, 20, 25–43. Both authors together wrote the entire key.

SELECTED REFERENCES Greven, H. C. 1999. A synopsis of *Grimmia* in Mexico, including *Grimmia mexicana*, sp. nov. *Bryologist* 102: 426–436. Greven, H. C. 2003. *Grimmiads of the World*. Leiden. Sayre, G. 1952. Key to the species of *Grimmia* in North America. *Bryologist* 55: 251–259.

1. Costa ending well before the apex; leaf tip rounded to cucullate, muticous; lamina uniformly 1-stratose; laminal cells all quadrate 42. *Grimmia mollis*
1. Costa reaching apex; leaf tip rounded to acute, muticous or awned; lamina usually with 2-stratose areas towards margins or with 2-stratose ridges; laminal cells oblate, quadrate, rectangular or elongate.
 2. Seta eccentrically attached to capsule base; capsule immersed, smooth, ventricose; stomata 3–4, large, at base of capsule (subg. *Gasterogrimmia*).
 3. Distal leaves concave-keeled; distal lamina 1-stratose or with 2-stratose patches, margins 1- or 2-stratose; annulus absent or reduced to 1–2 rows of small cells; operculum mammillate.
 4. Peristome present, annulus absent; distal lamina 1-stratose, margins 1- or 2-stratose 1. *Grimmia plagiopodia*
 4. Peristome absent, annulus present; distal lamina 1-stratose with 2-stratose patches, margins 2-stratose 2. *Grimmia anodon*
 3. Distal leaves concave; distal lamina 2-stratose with 2-stratose margins; annulus prominent; operculum rostrate.
 5. Basal laminal cells thick-walled; gonioautoicous; peristome fully developed 3. *Grimmia americana*
 5. Basal laminal cells thin-walled; dioicous; peristome rudimentary 4. *Grimmia crinitoleucophaea*

[2. Shifted to left margin.—Ed.]

2. Seta centrally attached to capsule base; capsule immersed to exserted, smooth to plicate, not ventricose; stomata none to many, small, at neck to base of capsule.
6. Leaves merely 1-stratose distally; margins at most narrowly 2-stratose; one or both leaf margins recurved (*G. reflexidens* plane) (mostly subg. *Rhabdogrimmia*).
 7. Costa projecting on abaxial side with two wings 39. *Grimmia ramondii*
 7. Costa on abaxial side smooth or angled.
 8. Leaves muticous, without awns or only distal leaves with very short awn or hyaline tip.
 9. Leaves cucullate 17. *Grimmia atrata* (in part)
 9. Leaves not cucullate.
 10. Leaves squarrose when moist; medial laminal cells oblate to rounded quadrate 34. *Grimmia lisae* (in part)
 10. Leaves erect to patent when moist; medial laminal cells quadrate to short-rectangular.
 11. Basal marginal cells with thickened transverse walls; seta arcuate; globular gemmae occasionally present on leaves 41. *Grimmia trichophylla* (in part)
 11. Basal marginal cells with thin transverse walls; seta straight or slightly arcuate; gemmae absent
 12. One leaf margin recurved; medial laminal cells sinuose; seta straight or slightly arcuate 9. *Grimmia elongata*
 12. Leaf margins both recurved; medial laminal cells with nodulose walls; seta straight 25. *Grimmia lesherae*
 8. At least distal or perichaetial leaves with distinct awns.
 13. Awns nearly equal to or much longer than lamina, decurrent, seta straight to flexuose.
 14. Awns 1–2 mm, leaf margins plane, [seta straight]; only known from Maritime provinces in North America 12. *Grimmia reflexidens*
 14. Awns 2–4 mm, leaf margins both recurved; seta flexuose; endemic to Montana and Idaho 28. *Grimmia brittoniae*
 13. Awns typically shorter than lamina (*G. pulvinata* can be long); decurrent or not; seta arcuate to cygneous.
 15. Leaves abruptly narrowed to awns, apex rounded; autoicous.
 16. Operculum rostrate; basal marginal laminal cells quadrate to short-rectangular 38. *Grimmia pulvinata*
 16. Operculum mammillate to conical; basal marginal laminal cells short- to long-rectangular.
 17. Awns only on perichaetial leaves; basal juxtacostal cells with thin, straight walls; marginal distal lamina 2-stratose; acidic rocks 35. *Grimmia moxleyi*
 17. Awns on all distal leaves; basal juxtacostal cells with thick, nodulose walls; marginal distal lamina 1-stratose; basic rocks 37. *Grimmia orbicularis*
 15. Leaves gradually tapering to awns, apex narrowed; dioicous.
 18. Clusters of gemmae easily visible on abaxial side of leaf lamina or on leaf tips.
 19. Multicellular gemmae on abaxial side of leaf lamina in distal leaves; leaves crisped and contored 40. *Grimmia torquata*
 19. Cluster of gemmae only on leaf tips; leaves straight.
 20. Leaves with blunt eroded apices; distal cells with pseudo-papillose walls; stem central strand present 26. *Grimmia anomala*
 20. Leaves with acuminate apices; distal cells with smooth walls; stem central strand absent 31. *Grimmia bartmanii*

18. Clusters of gemmae absent or in obscure clusters in leaf axils.
21. Leaves narrowly ovate-lanceolate to linear-lanceolate, distinctly incurved or contorted when dry 32. *Grimmia incurva*
21. Leaves lanceolate to ovate-lanceolate, straight, appressed, only occasionally somewhat contorted when dry.
22. Central strand absent; basal juxtacostal leaf cells uniformly elongate to linear, strongly nodulose and thick-walled; mid leaf cells extremely sinuose and very thick-walled; leaf margins both recurved.
23. Costa circular, projecting in transverse section; basal marginal cells thin-walled; distal leaves straight, awns not decurrent 27. *Grimmia attenuata*
23. Costa semicircular, not projecting in transverse section; basal marginal cells thick-walled; distal leaves often secund, awns often decurrent 33. *Grimmia leibergii*
22. Central strand present; basal juxtacostal cells short- to long-rectangular, elongate cells absent or few and scattered; mid leaf cells straight to sinuose, thin- to thick-walled; leaf margins one or both recurved.
24. Leaves squarrose when moist; mid leaf cells rounded to oblate, straight 34. *Grimmia lisae* (in part)
24. Leaves erect to patent when moist; mid leaf cells rounded-quadrate to short-rectangular, sinuose.
25. Blackish green tufts; costa angled or bluntly winged in transverse section; awns denticulate, occasionally decurrent; capsule globose, brown 36. *Grimmia muehlenbeckii*
25. Yellowish green tufts; costa semicircular in transverse section; awns smooth to slightly denticulate, not decurrent; capsule oblong-ovoid, yellow-green 41. *Grimmia trichophylla* (in part)
- [6. Shifted to left margin.—Ed.]
6. Leaves 2–3-stratose distally or 1-stratose with distal margins widely 2-stratose (*G. sessitana* and some *G. donniana*); leaf margins incurved, plane or recurved.
26. Leaves concave; costa not prominent; margins plane or incurved; dioicous (subg. *Litoneuron*).
27. All leaves muticous, straight or falcate.
28. Leaves oblong-lanceolate to ligulate, straight, cucullate, obtuse-rounded; basal marginal laminal cells short-rectangular; widely distributed 18. *Grimmia unicolor*
28. Leaves oblong-lanceolate, homomallous-falcate, subulate, uncinata; basal marginal laminal cells quadrate to short-rectangular; endemic to Pacific Coast region. 19. *Grimmia hamulosa*
27. At least distal leaves awned, straight.
29. Leaves oblong-ovate to oblong-lanceolate; basal marginal laminal cells oblate to quadrate; costa broad at base; awn broadly attached and decurrent . . 24. *Grimmia laevigata*
29. Leaves ovate-lanceolate from an ovate base; basal marginal laminal cells quadrate to long-rectangular; costa narrow at base; awn typically narrowly attached and not decurrent.
30. Costa-like multistratose leaf bands present in transverse section 23. *Grimmia serrana*
30. Costa-like multistratose leaf bands absent.

31. Capsule emergent, gymnostomous, stomata absent, operculum mammillate; basal laminal cells uniformly short-rectangular, straight and thin-walled 22. *Grimmia nevadensis*
31. Capsule exerted, peristome fully developed, stomata present, operculum rostrate; basal marginal and juxtacostal laminal cells typically contrasting in length or thickness.
32. Basal marginal laminal cells quadrate; basal juxtacostal laminal cells quadrate to short-rectangular; seta sigmoid; capsule wrinkled when dry; perichaetial leaves not enlarged; endemic to eastern North America 20. *Grimmia olneyi*
32. Basal marginal laminal cells quadrate to long-rectangular; basal juxtacostal laminal cells rectangular to elongate; seta straight; capsule smooth when dry; perichaetial leaves enlarged; widely distributed 21. *Grimmia ovalis*
- [26. Shifted to left margin.—Ed.]
26. Leaves keeled; costa prominent; margins recurved, plane or incurved; autoicous or dioicous (mostly subg. *Guembelia*).
33. Margins plane or incurved.
34. Costa transverse section circular distally; awn hyaline-tipped to short (0.3 mm), decurrent 13. *Grimmia teretinervis*
34. Costa transverse section semicircular distally; awn short to long, usually prominent, decurrent or not.
35. Seta arcuate; leaves spirally curved around stem when dry, flagelliform innovations present 30. *Grimmia funalis* (in part)
35. Seta straight; leaves straight when dry, flagelliform innovations absent.
36. Gemmae abundant on adaxial distal leaf surface 43. *Grimmia shastae*
36. Gemmae absent on leaves.
37. Distal laminal cells bulging.
38. Leaf margins plane; cladautoicous; basal juxtacostal laminal cells rectangular to elongate; distal juxtacostal laminal cells 1-stratose; stomata present 10. *Grimmia sessitana* (in part)
38. Leaf margins incurved; dioicous; basal juxtacostal laminal cells quadrate to short-rectangular; distal juxtacostal laminal cells 2-stratose; stomata present or absent.
39. Stomata absent; leaves not plicate, not cucullate 6. *Grimmia alpestris* (in part)
39. Stomata present; leaves weakly to rarely strongly plicate distally, cucullate 11. *Grimmia caespiticia*
37. Distal laminal cells not bulging.
40. Margins plane throughout; basal marginal laminal cells short- to long-rectangular; stomata present; autoicous.
41. Distal juxtacostal laminal cells 2-stratose, occasionally 1-stratose; basal marginal leaf cells long-rectangular, hyaline; annulus large, of 2 rows of rectangular cells, revoluble; calyptra mitrate 8. *Grimmia donniana*
41. Distal juxtacostal laminal cells 1-stratose; basal marginal leaf cells short- to long-rectangular, rarely hyaline; annulus small, of 1 row of quadrate cells, not revoluble; calyptra cucullate 10. *Grimmia sessitana* (in part)
40. Margins incurved distally; basal marginal laminal cells quadrate to short-rectangular; stomata absent; dioicous.
42. Capsule immersed to emergent, wide-mouthed, peristome rudimentary; endemic to California 7. *Grimmia mariniana*
42. Capsule exerted, narrow-mouthed, peristome present, fully developed; widespread in western North America.

43. Basal juxtacostal laminal cells short- to long-rectangular, distinct from quadrate to short-rectangular basal marginal cells; medial laminal cells rounded, thick-walled 5. *Grimmia montana*
43. Basal juxtacostal and marginal cells quadrate to short-rectangular, basal areolation relatively uniform; medial laminal cells quadrate to short-rectangular, thin-walled 6. *Grimmia alpestris* (in part)
- [33. Shifted to left margin.—Ed.]
33. Margins recurved on one or both sides.
44. Leaves muticous, cucullate 17. *Grimmia atrata* (in part)
44. Leaves awned, not cucullate.
45. Leaves spirally curved around stem when dry, flagelliform innovations present 30. *Grimmia funalis* (in part)
45. Leaves straight when dry, flagelliform innovations absent.
46. Sporophytes present.
47. Capsule immersed.
48. Stem central strand present, epidermis thin; leaf margins 2-stratose, not thickened, one margin recurved (rarely both); leaves broadly ovate-lanceolate 15. *Grimmia arizonae* (in part)
48. Stem central strand absent, epidermis thick; leaf margins 3(–4) stratose, thicker than juxtacostal lamina, usually both margins recurved; leaves narrowly lanceolate from an ovate base 16. *Grimmia pilifera* (in part)
47. Capsule exserted.
49. Seta arcuate; dioicous 29. *Grimmia elatior* (in part)
49. Seta straight; autoicous.
50. Annulus small, 1 row of quadrate cells; stomata in 1 row; basal juxtacostal cells straight and thin-walled 10. *Grimmia sessitana* (in part)
50. Annulus prominent, 2 rows of rectangular cells; stomata in 2–3 rows; basal juxtacostal cells sinuose and thick walled 14. *Grimmia longirostris* (in part)
46. Sporophytes absent.
51. Basal juxtacostal cells straight, thin-walled; distal juxtacostal lamina 1-stratose, cells often bulging; plants small (less than 1 cm), blackish; moist, alpine habitats 10. *Grimmia sessitana* (in part)
51. Basal juxtacostal cells sinuose, thick-walled; distal juxtacostal lamina at least 2-stratose, cells not bulging; plants robust (greater than 1 cm), yellow-green to very dark olivaceous; dry, widely distributed.
52. Leaf margins 2-stratose, not thickened; stem central strand present, epidermis thin.
53. Autoicous; costa transverse section reniform; leaves sheathing; widely distributed 14. *Grimmia longirostris* (in part)
53. Dioicous; costa transverse section semicircular; leaves not sheathing; American Southwest 15. *Grimmia arizonae* (in part)
52. Leaf margins multistratose and thickened; stem central strand absent, epidermis thick.
54. Leaves narrowly lanceolate from an ovate base, usually narrowly recurved on both margins; distal lamina without multistratose bands, never papillose 16. *Grimmia pilifera* (in part)
54. Leaves broadly lanceolate, broadly recurved on one margin; distal lamina with multistratose bands, occasionally papillose 29. *Grimmia elatior* (in part)

2a. GRIMMIA subg. GASTEROGRIMMIA Schimper, Coroll. Bryol. Eur., 46. 1856

Plants to 15 mm. **Stem** central strand strong. **Leaves** oblong-ovate to oblong-lanceolate, keeled or concave, margins plane, costa prominent; juxtacostal and marginal basal laminal cells hyaline; distal lamina 2-stratose (1-stratose for *G. plagiopodia*). **Gemmae** absent. **Sexual condition** autoicous (*G. crinitoleucophaea* dioicous). **Seta** arcuate to sigmoid (except *G. americana*), eccentrically attached to capsule. **Capsule** immersed, smooth, ventricose; stomata 3–4, large, at base of capsule. **Calyptra** mitrate, just covering operculum.

Species 4 (4 in the flora): North America, Mexico, Central America, South America, Eurasia, n Africa, Pacific Islands (New Zealand), Australasia, Antarctic.

Members of subgenus *Gasterogrimmia* are recognized by their commonly occurring immersed, ventricose capsules on arcuate to sigmoid setae that are eccentrically attached. Additionally, all these species have three to four large stomata at the very base of the capsule. The entire basal region of the leaf is typically hyaline. Most members of the subgenus are restricted to calcareous habitats. The genus *Jaffueliobryum* is the only other group in the Grimmiaceae to be so strongly tied to calcareous substrates.

1. *Grimmia plagiopodia* Hedwig, Sp. Musc. Frond., 78, plate 15, figs. 6–13. 1801



Grimmia brandegeei Austin

Plants in dense cushions to hoary tufts, dark green to brown. **Stems** 0.3–0.5(–1) cm. **Leaves** oblong-ovate, 1–1.7 × 0.4–0.8 mm, concave-keeled, awn 0.3–1 mm; basal juxtacostal laminal cells quadrate to short-rectangular, straight, thin-walled; basal

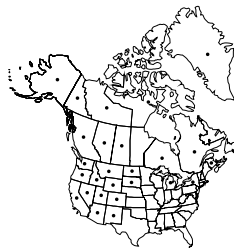
marginal laminal cells quadrate to short-rectangular, straight, thin-walled; medial laminal cells quadrate to short-rectangular, slightly sinuose, slightly thick-walled; distal laminal cells 1-stratose, marginal cells 1–2-stratose. **Sexual condition** gonioautoicous. **Seta** sigmoid, 0.2–0.3 mm. **Capsule** usually present, exothecial cells thin-walled, annulus absent, operculum mammillate, peristome present, fully developed, perforated and split in distal half.

Exposed calcareous sandstone, limestone, occasionally concrete, and glacio-lacustrine silt; low to high elevations (50–2400 m); Greenland; Alta., B.C., N.W.T., Nunavut, Ont., Sask.; Alaska, Calif., Colo., Idaho, Ill., Iowa, Minn., Mont., Nebr., Nev., N.Mex., N.Dak., S.Dak., Utah, Wis., Wyo.; South America; Eurasia; Pacific Islands (New Zealand); Antarctic.

Grimmia plagiopodia has a widespread and continuous distribution on calcareous rock across the northern Great Plains, reaching as far east as Illinois. It is rare in eastern North America, with a disjunct site in southern Ontario. In the west it reaches into the mountains on limestone and basic sandstone deposits,

but its continuous range does not extend west of a line from Utah to south-central British Columbia. There is a disjunct location near Carson City, Nevada and Lake Tahoe, California. In the Arctic it is known from a few scattered localities extending from northwestern Greenland and nearby Ellesmere Island to the North Slope of Alaska. Compared to *G. anodon*, *G. plagiopodia* tends to occupy more prairie-like sites and is typically found at lower elevations. Commonly fertile, it is recognized by its immersed, peristomate capsule on a sigmoid seta with fully-developed teeth that are perforated and split distally. *Grimmia americana* is similar but has a short, straight to arcuate seta and a large annulus. The other widespread species in the group, *G. anodon*, has an annulus and is gymnostomous.

2. *Grimmia anodon* Bruch & Schimper, Bryol. Europ. 3: 110. 1845



Grimmia anodon var. *anomala* Bartram; *G. subanodon* Ochyra; *Schistidium obtusifolium* Ireland & H. A. Crum

Plants in small cushions, dark green to brown. **Stems** 0.5–1 cm. **Leaves** oblong-ovate to oblong-lanceolate, 0.9–2 × 0.4–0.8 mm, concave-keeled, awn 0.1–1.2 mm;

basal juxtacostal laminal cells quadrate to long-rectangular, straight, thin-walled; basal marginal laminal cells quadrate to long-rectangular, straight, thin-walled; medial laminal cells quadrate, sinuose, thick-walled; distal laminal cells 1-stratose with 2-stratose patches, marginal cells 2-stratose. **Sexual condition** gonioautoicous. **Seta**

sigmoid, 0.2–0.3 mm. **Capsule** usually present, exothelial cells thin-walled, annulus of 1–2 rows of quadrate, thin-walled cells, not revoluble, operculum mammillate, peristome absent.

Exposed, calcareous sandstone, limestone, and concrete; low to high elevations (20–2700 m); Greenland; Alta., B.C., N.B., N.W.T., Nunavut, Ont., Que., Sask., Yukon; Alaska, Ariz., Calif., Colo., Idaho, Mich., Mont., Nev., N.Mex., N.Y., N.Dak., Oreg., S.Dak., Utah, Wash., Wyo.; ne Mexico; South America (Bolivia, Chile); Eurasia; Africa (Morocco).

Grimmia anodon is widespread and common across the western United States and the mountains of southern Alberta and British Columbia. It is absent from eastern North America except around the Great Lakes and individual sites in the Gaspé Peninsula and New Brunswick. It extends sparsely into the Yukon and Alaska. These high latitude sites are strongly correlated with glacial refugia or areas of early deglaciation. Most eastern United States collecting localities are near the margin of the Wisconsinan continental ice sheet. The west-east disjunction of the species suggests the disruption of a more continuous distribution by Wisconsinan glacial events. It is widespread elsewhere in the northern hemisphere on calcareous outcrops and disturbed sites. Usually fertile, *G. anodon* is recognized easily by its immersed, gymnostomous capsule, on a sigmoid seta. The other widespread species in the subgenus, *G. plagiopodia*, has peristome teeth. When sterile these species can be difficult to differentiate, but *G. anodon* has leaves that are more concave with 2-stratose margins, while leaves of *G. plagiopodia* tend to be more keeled and are more uniformly 1-stratose. *Grimmia anodon* is rather similar to *Schistidium flaccidum*. However, the latter is characterized by a short, straight seta, leaves sharply keeled distally, and leaf margins plane at base but recurved distally on both sides.

3. *Grimmia americana* E. B. Bartram, Bryologist 32: 8, fig. 1. 1929 [C][E][F]



Plants in hoary tufts, dark green to brown. **Stems** 0.5–1.5 cm. **Leaves** oblong-ovate to oblong-lanceolate, 1.5–2 × 0.5–0.9 mm, concave, awn to 1 mm; basal juxtacostal laminal cells quadrate to short-rectangular, straight, thick-walled; basal marginal laminal cells quadrate to long-rectangular, straight, thick-walled, medial laminal cells rounded-quadrate, slightly thick-walled; distal laminal cells 2-stratose, marginal cells 2-stratose. **Sexual condition** gonioautoicous. **Seta** straight to arcuate, 0.6–1 mm. **Capsule** usually present, exothelial cells thick-

walled, annulus of 2–3 rows of rectangular, thin-walled cells, revoluble, operculum rostellate, peristome present, fully developed, perforated and split in most distal part, weakly papillose.

Calcareous rock; moderate to high elevations (ca. 1600 m); of conservation concern; Ariz., Nev., Tex.

Grimmia americana is a rare endemic, currently known only from three sites. Until 1999, the species was known only from its type locality in Jeff Davis County of western Texas. A second locality was reported by J. Muñoz (1999) in Arizona and a third site by L. R. Stark et al. (2002) in Nevada. Thus, it is reasonable to expect *G. americana* to occur also in southern New Mexico. It is recognized as a member of subg. *Gasterogrimmia* by its immersed, ventricose capsule, with a short mitrate calyptra and eccentric seta attachment. The overall habit of the species also is similar to that of the other members of the subgenus. However, its basal laminal cells are thick-walled while other members have thin cell walls. H. A. Crum (1994c) implied that *G. americana* is similar to *G. anodon*, but the former is readily separated by its fully developed, perforated peristome, rostellate operculum, and thick-walled basal laminal cells. *Grimmia crinitoleucophaea*, also most commonly found in the American Southwest, is dioicous, has a rudimentary peristome, and thin-walled basal laminal cells.

4. *Grimmia crinitoleucophaea* Cardot, Rev. Bryol. 17: 18. 1890



Plants in loose tufts, olivaceous to black. **Stems** 0.5–0.9 cm. **Leaves** oblong-ovate to oblong-lanceolate, 1.6–2 × 0.3–0.6 mm, concave, awn 0.3–0.6 mm; basal juxtacostal laminal cells quadrate to long-rectangular, straight, thin-walled; basal marginal laminal cells quadrate to short-rectangular, straight, thin-walled; medial laminal cells rounded, straight, thick-walled; distal laminal cells 2-stratose, marginal cells 2-stratose. **Sexual condition** dioicous. **Seta** sigmoid, 0.3–0.5 mm. **Capsule** usually present, exothelial cells thin-walled, annulus of 2–3 rows, rectangular, thick-walled, revoluble, operculum obliquely rostrate, peristome present, rudimentary, teeth composed of only a few rows of cells, perforated, papillose.

Basalt, granite, schist and limestone; moderate to high elevations (500–2100 m); B.C., N.W.T., Yukon; Ariz., Calif., Colo., Nev., N.Mex., Utah, Wash.; Eurasia.

In North America, *Grimmia crinitoleucophaea* is known from only scattered localities in the American west and in three extremely disjunct sites in Canada: in southern British Columbia, near the Keele River of the Northwest Territories, and along the Dempster Highway

in the Yukon. It is found on a broad range of both basic and acidic rock types. Its subgeneric placement is problematic. Gametophytically the species is inseparable from *G. tergestina*, of subg. *Litoneuron*. Indeed, based on areolation and leaf shape, L. Loeske (1913–1914, part 1) placed it as a subspecies of the latter. This close similarity may account for reports by J. Muñoz and F. Pando (2000) and D. H. Norris and J. R. Shevock (2004) of *G. tergestina* from North America. We have seen all cited specimens in these papers and they all represent *G. cunitoleucophaea* or *G. ovalis*. Therefore, we reject *G. tergestina* being in North America. Sporophytic characters of *G. cunitoleucophaea* (a short, arcuate to

sigmoid seta that is eccentrically attached to the capsule, an immersed ventricose capsule with a small, mitrate calyptra, and 3–4 large stomata) clearly indicate membership in subg. *Gasterogrimmia*. Further, *G. cunitoleucophaea* and *G. tergestina* have never been collected together, suggesting that the two are also ecologically distinct. Despite its dioicous sexuality, *G. cunitoleucophaea* is usually fertile; its rudimentary peristome and large annulus are thus readily evident. Its 2-stratose laminal stratification separates it from specimens of *G. plagiopodia* that may have broken peristome teeth.

2b. GRIMMIA subg. GUEMBELIA (Hampe) Schimper, Coroll. Bryol. Eur., 48. 1856

Guembelia Hampe, Bot. Zeitung (Berlin) 4: 124. 1846

Plants 10–20 mm (–70 mm for *G. atrata*). **Stem** central strand present or absent. **Leaves** narrowly ovate-lanceolate to oblong-lanceolate, keeled, margins plane, recurved or incurved, costa prominent; basal marginal cells hyaline or not; distal lamina 2-stratose or with at least several marginal rows 2-stratose. **Gemmae** absent. **Sexual condition** autoicous or dioicous. **Seta** straight, centrally attached to capsule. **Capsule** immersed to exserted, smooth (except *G. mariniana*); stomata present or absent, small, at neck to part way up capsule. **Calyptra** mitrate to cucullate, covering operculum.

Species 41 (13 in the flora): North America, Mexico, Central America, South America, Eurasia, Africa, Pacific Islands, Australia, Antarctic.

Members of subg. *Guembelia* are recognized by their thick, keeled leaves and usually long, straight setae with smooth capsules. Most occur on dry acidic rock, with three species growing on damp to wet acidic rock and one on dry calcareous rock.

5. *Grimmia montana* Bruch & Schimper, Bryol. Europ. 3. 128. 1845



Grimmia arctophila Kindberg;
G. brachydon Austin; *G. jamesii*
 Austin; *G. montana* var. *brachydon*
 (Austin) Lesquereux & James;
G. tenella (Müller Hal.) Kindberg;
Guembelia tenella Müller Hal.

Plants in hoary cushions, yellow-green to dark blue-green, sometimes almost black. **Stems** 1–1.2(–1.5) cm, central strand weak. **Leaves** narrowly lanceolate, rarely ovate-lanceolate, 1–2 × 0.3–0.6 mm, concave-keeled, not plicate, margins plane, usually narrowly incurved distally, awn 0.2–1.3 mm, costal transverse section not prominent to prominent, semicircular; basal juxtacostal laminal cells short- to long-rectangular, straight, thick-walled; basal marginal laminal cells quadrate to short-rectangular, straight, thick-walled,

not hyaline; medial laminal cells rounded, thick-walled; distal laminal cells 2-stratose, not bulging, marginal cells 2-stratose, not bulging. **Sexual condition** dioicous, perichaetial leaves not enlarged. **Seta** straight, 2–3 mm. **Capsule** occasionally present, exserted, yellow to brown, oblong, exothelial cells rectangular, thin-walled, stomata absent, annulus of 1 row of quadrate, thick-walled cells, operculum rostellate, peristome present, fully developed, split and perforated in distal half.

Exposed acidic granite and sandstone; moderate to high elevations (900–4000 m); Greenland; Alta., B.C., Nunavut, Ont., Yukon; Alaska, Ariz., Calif., Colo., Idaho, Mont., Nev., N.Mex., Oreg., Utah, Wash., Wyo.; Mexico; Europe; Africa.

Grimmia montana is widespread and common on acidic rock in the warm, dry, western interior of North