

Gymnostomum aeruginosum, *G. calcareum* and *G. viridulum* (Pottiaceae, Bryopsida) in California

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SUMMARY

Recent discoveries of true *Gymnostomum calcareum* Nees & Hornsch. and *G. viridulum* Brid. in California, U.S.A., prompted a new look at the genus in America. Perichaetia borne laterally on short branches, perichaetial leaves strongly differentiated from the cauline, and bulging exothecial cells are critical new traits introduced here to distinguish both species from *G. aeruginosum*. All three species may have distal laminal margins bistratose in patches.

KEYWORDS: *Anoetangium*, California, exothecial cells, *Gymnostomum calcareum*, *Gymnostomum viridulum*.

INTRODUCTION

Continuing bryological research in the state of California, U.S.A., by several very active bryologists, has turned up material of *Gymnostomum* Nees & Hornsch. (Pottiaceae, Bryopsida) with both gemmae and unexpected sexual structures similar to those of *Anoetangium* Schwägr. in addition to oddly bulging capsule exothecial cells. This prompted a re-examination of previous publications by the first author and a study of authentic European material, which supported recognition of *G. calcareum* Nees & Hornsch. and *G. viridulum* Brid. for the New World.

Gymnostomum calcareum has been widely reported for North America, but Crum and Anderson (1956), after considerable study, indicated that all reports were *G. aeruginosum* Sm. Zander (1977), in a study of Central American and Mexican *Gymnostomum*, even synonymized the two species citing complete intergradation of all features. This was rejected by European authors Newton (1983), Whitehouse and Crundwell (1992) and Sérgio (2006). Although Whitehouse and Crundwell reported that specimens of the three species of *Gymnostomum* studied retain their traits in cultivation, genetic differentiation associated with microhabitats within a species is to be expected, perhaps maintained by balancing selection.

Both *G. aeruginosum* and *G. calcareum* occasionally have distal patches or large sections of bistratose distal laminal cells marginally and occasionally also medially in North America, and this is true, apparently, for both the former

species (Newton, 1983; Smith, 2004) and the latter (Guerra, 2004) in Europe. Sérgio (2006) decided that bistratose laminae are of no taxonomic value in the genus. The newly described western European taxa *G. aeruginosum* var. *obscurum* J. Guerra (Guerra, 2004) and *G. lanceolatum* M.J.Cano, Ros & J.Guerra, however, are distinguished in large part by this trait. The former taxon is matched by much North American material, and is here considered synonymous; the latter taxon requires additional study. The similar range of variation in presence and extent of laminal bistratosity in species of other genera of the Pottiaceae supports by extension the idea that the patchy bistratose laminal condition in *Gymnostomum* is not strikingly unusual or well correlated with other characters.

Worldwide, there seems to be a spectrum of variation in *Gymnostomum* grading from plants with large stature (*G. aeruginosum*) to the smallest (*G. mosis* (Lorentz) Jur.). To determine whether expression of variation in critical traits is perhaps in part independent and associated with plastic response and also linked and incremental but minor, genetically based phenovariation correlated with various microhabitats, or fairly stable and distinguished genetic trait clusters associated with major adaptive solutions to environmental challenges is a desideratum, and future revisions of the genus desperately need biosystematic analysis. It is the opinion of the first author that there are only three taxa of *Gymnostomum* in California, although individual specimens might be assigned other names based on Guerra's (2005) treatment of European representatives

of the genus. Occasional specimens of *Hymenostylium recurvirostrum* (Hedw.) Dixon with a blunt leaf apex and quadrate distal medial laminal cells that are densely papillose are similar to *Gymnostomum* species, but the former species usually exhibits much deeper turf and lacks a stem central strand. From *Gymnostomum aeruginosum* it further differs in the elongate adaxial costal cells.

Gymnostomum may be described briefly as follows. *Plants* very small to medium in stature, in dense cushions or expanded sods, ferruginous below, glaucous-green to vivid emerald green above. *Leaves* appressed to incurved or somewhat twisted and contorted when dry, spreading when moist; margins entire or minutely papillose-crenulate; distal cells papillose, basal cells elongate and mostly smooth; costa usually ending shortly before the apex, adaxial cells quadrate to very short-rectangular but elongate in small leaves. *Sexual condition* dioicous. *Seta* elongate. *Capsule* light to dark brown, ovoid to oblong-ovoid, smooth or colliculate, mouth slightly constricted; operculum long-conic; peristome absent. *Calyptra* cucullate. The species commonly occur on wet to dry cliffs and boulders containing lime.

KEY TO SPECIES OF *GYMNOSTOMUM* IN CALIFORNIA

1 Exothecial cells flat or weakly convex, usually 20–25(–30) μm wide; perichaetia single on an axis, terminating the axis, perichaetial leaves ligulate to ovate-lanceolate, with laminal cells beyond the base quadrate and strongly papillose; cauline leaves long-rectangular or long-elliptical to broadly lanceolate, 0.5–1(–1.5) mm, distal adaxial costal cells quadrate to very short-rectangular; plants usually loosely caespitose, occasionally crowded, rarely forming a dense turf

G. aeruginosum

1 Exothecial cells usually bulging, commonly 30–40 μm wide; perichaetia often multiple on an axis, terminating short or rather elongate lateral branches, perichaetial leaves narrowly lanceolate to triangular, with all or most cells elongate, rectangular to rhomboidal, smooth or weakly papillose; cauline leaves long-rectangular to short-elliptic, usually 0.3–0.6 mm, distal adaxial costal cells usually elongate, occasionally short-rectangular; plants often forming a dense turf

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2 Gemmae absent from leaf axils; leaves 0.4–0.6 mm; plants light green above, capsules elliptic, narrow-mouthed, with a distinct circumstomal collar; cauline leaves rectangular to elliptic, occasionally ovate

G. calcareum

2 Gemmae present in leaf axils; leaves 0.3–0.4(–0.6) mm; plants dark green above; capsules short-cylindric, wide-mouthed, lacking a circumstomal collar; cauline leaves short-elliptic or ovate

G. viridulum

1. *Gymnostomum aeruginosum* Sm., *Flora Britannica* 3: 1163. 1804.

Relevant synonymy:

Gymnostomum rupestre Schwägr., *Spec. Musc. Frond.*, *Suppl.* 1, 1: 31. 1811.

Gymnostomum gracillimum Nees & Hornsch., *Bryol. Germ.* 1: 149. 1823.

Gymnostomum tophaceum Austin, *Bull. Torrey Bot. Club* 6: 42. 1875.

Gymnostomum clintonii Austin, *Bull. Torrey Bot. Club* 6: 42. 1875.

Anoetangium arizonicum E. B. Bartram, *Moss Flora of North America* 1: 192. 1938.

Gymnostomum aeruginosum var. *obscurum* J. Guerra in C. Sérgio & M. J. Cano, *Flora Briof. Ibér.*, *Pottiaceae: Eucladium, Gymnostomum, Gyroweisia, Hymenostylium, Leptobarbula*. 10. 2004, *syn. nov.*

Plants light to dark green, caespitose, crowded or rarely forming a dense turf. *Cauline leaves* long-rectangular or long-elliptical to broadly lanceolate, straight to strongly reflexed, 0.5–1.5 mm, apex rounded to broadly acute, occasionally apiculate; distal cells sometimes bistratose marginally in patches or entirely and also medially in patches, distal laminal cells 7–13 μm in width, 1 : 1; distal adaxial costal cells quadrate to very short-rectangular. *Specialised asexual reproduction* absent. *Perichaetia* single on an elongate axis, terminating the axis; perichaetial leaves loose and flexuose, ligulate to ovate-lanceolate, little sheathing at base, basal cells rectangular, smooth, distal laminal cells quadrate, strongly papillose. *Capsule* long- or rarely short-cylindric, wide-mouthed, with flat or weakly convex exothecial cells, these usually 20–25(–30) μm wide, though somewhat bulging near the neck. Sterile in California.

Calcareous rock in wet situations, especially near waterfalls, moist gorge walls, rarely soil, near sea level to 3000 m in North America. Distribution: California and most states of U.S.A., nearly worldwide.

Representative specimens examined: U.S.A. California. Humboldt Co., *Duell 1988/1* (MO, UC). *Austria.* Salzburg. ‘Gymnost. gracillimum Hornschuch. Alp. Salzburg,’ no date (E; Arnott collection, two specimens identified as isotypes of *Gymnostomum gracillimum* by ‘S.R.R. 05’); Salzburg, ‘versus Huetttau’, no date (B-isotype of *Gymnostomum gracillimum*).

Although fertile and fruiting material have not yet been located, *Gymnostomum aeruginosum* is present in at least northern California judging from the relatively large size of the plants (turf to 1 cm deep, cauline leaves commonly >0.5 mm) and the broadly lanceolate to ligulate leaves with quadrate adaxial costal cells. Small forms of *Gymnostomum aeruginosum* in other parts of the country may be similar to *G. viridulum* in the short-cylindric capsule, but the capsules are shorter, ca 0.4 mm, exothecial cells not bulging, the perichaetial leaves are not well differentiated, and gemmae are lacking. Generally, however, the capsules of *G. aeruginosum* are usually about as long as those of *G. calcareum* and *G. viridulum*, with urns about 1.4–1.8 mm in length.

2. *Gymnostomum calcareum* Nees & Hornsch., *Bryologia Germanica* 1: 153. pl. 10 f. 15. 1823. TYPE: Austria, Salzburg, ‘Salzburg, Hornschuch 1824’, specimen ‘a’ (E; Greville Herbarium, isotype of *Gymnostomum calcareum*).

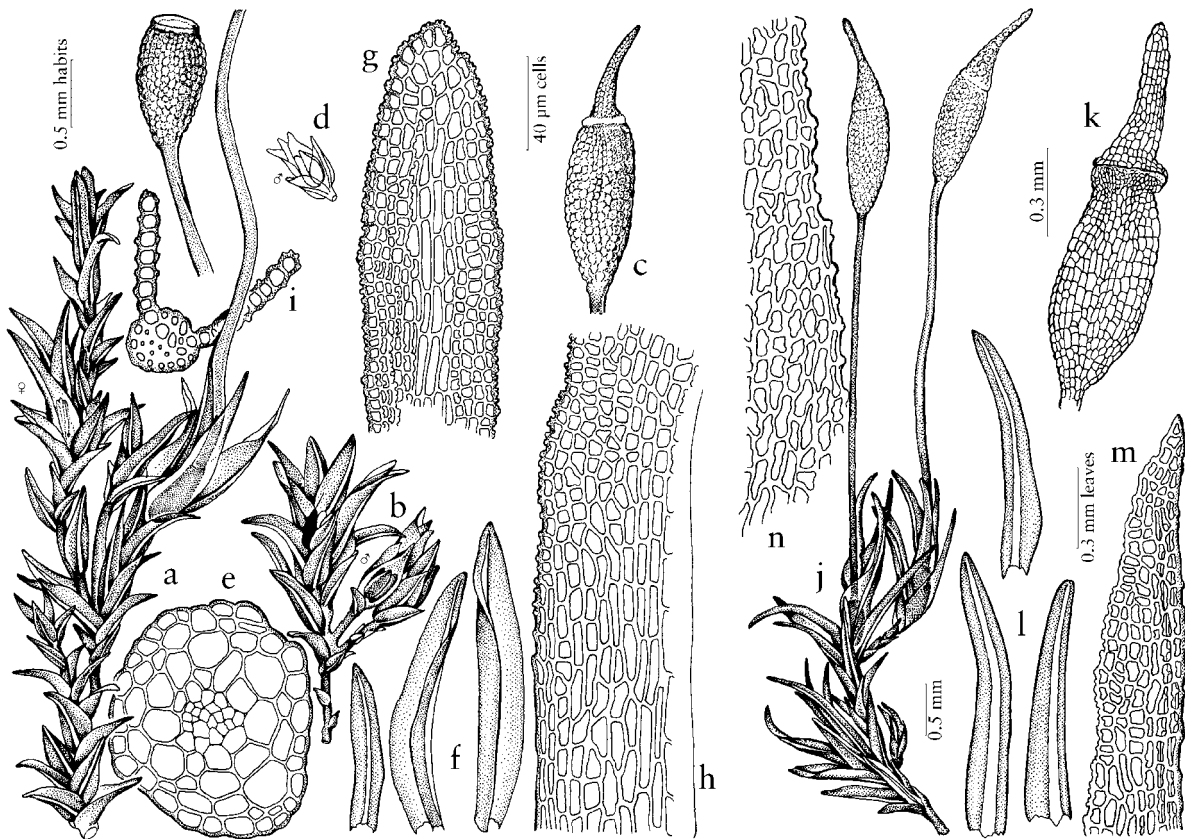


Figure 1. (a–i) *Gymnostomum calcareum*, California, Habeeb 1307: (NY.), (a) fruiting plant; (b) perigonal plant; (c) operculate capsule; (d) perigonal bud; (e) stem transverse section; (f) three cauline leaves; (g) leaf apex; (h) leaf basal cells; (i) transverse section of leaf. (j–n) *Gymnostomum calcareum*, probable isotype, Austria, 'Hornsch. 1824': (j) fruiting plant; (k) capsule; (l) three cauline leaves; (m) cauline leaf apex; (n) medial laminal cells, perichaetial leaf.

Plants light to dark green, loosely caespitose, crowded or sometimes forming a dense turf. *Cauline leaves* long-rectangular or less commonly lanceolate, straight to weakly reflexed apically, 0.4–0.6(–0.8) mm, apex rounded to broadly acute, occasionally apiculate; distal marginal cells sometimes bistratose in patches, distal laminal cells 5–8(–10) μm in width, 1–2 : 1; distal adaxial costal cells usually elongate, occasionally short-rectangular, rarely quadrate in a central patch. *Specialized asexual reproduction* absent (at least in California). *Perichaetia* often multiple on an axis, terminating short or rather elongate lateral branches; perichaetial leaves usually stiff and often second, narrowly lanceolate to triangular, commonly with all cells elongate, rectangular to rhomboidal, smooth or weakly papillose, occasionally quadrate distally but then perichaetial leaves lanceolate or very strongly sheathing in proximal half. *Capsule* elliptical, with a circumstomal collar and bulging exothecial cells, usually 30–40(–50) μm wide.

Capsules mature spring. Damp cliff faces and wet rocks near waterfalls, at 150–650 m in California. Distribution: U.S.A. in California, Missouri, North Carolina; Mexico in Tamalipas; South America; Eurasia; Africa; Atlantic Islands (Azores, Canary Islands); Pacific Islands (New Zealand); Indian Ocean Islands (Réunion); Australia.

Vegetatively, *Gymnostomum aeruginosum* grades into *G. calcareum* at least in North America, with *G. calcareum* occurring more often in tight turfs, being generally a smaller plant, often with strict cauline leaves having rounded leaf apices and sides nearly parallel, and distal laminal cells slightly smaller. Leaves of sterile plants 0.4–0.6 mm; leaves of perichaetiate plants commonly somewhat longer, to 0.8 mm or more. Aside from these weak traits, there are sharp differences in the inflorescence and capsules. The perichaetia are borne laterally off the main axis, terminating a short branch. This branch is somewhat longer than that supporting the perichaetium of *Anoetangium*, thus the branching arrangement is not quite as clearly monopodial as is the case with *Anoetangium*. The perichaetial bracts are also much like those of *Anoetangium*, with shape and areolation quite different from those of the cauline leaves. *Hymenostylium recurvirostrum*, with similarly differentiated perichaetial leaves, may, in mixture with sterile *G. aeruginosum*, falsely signal *G. calcareum*, but the former is definitively distinguished by the stem section showing a central cylinder of similar medium-sized cells and no central strand, while *Gymnostomum* species all have large cells in the central cylinder grading quickly into a small central strand. The capsule of *G. calcareum* usually has a distinct constricted

circumstomal collar, bulging exothelial cells, 25–35(–50) μm wide, and a weak or absent neck, while in *G. aeruginosum* the collar is not evident or is not constricted, the exothelial cells are smooth or weakly bulging, ca 20–25 μm wide, often bulging near the neck, and the neck of the capsule is usually well developed though flaccid. Because the capsules have the appearance of very young capsules of *G. aeruginosum* or those arrested in development by damage, the trait may be neotenic. In occasional specimens of *G. calcareum*, the capsule is clearly that of *G. aeruginosum*, and a dominant-recessive gene may be involved.

Authentic European specimens of *G. calcareum* exhibit these traits. An apparent isotype of *G. calcareum* from Salzburg, Austria, at E ('Bryol. Germ. t. 10. f. 15. Hornsch. 1824', specimen 'a') was annotated by D. G. Long (Nov. 1982) as 'Almost certainly isotype (probably collected 1823 or earlier and sent to Greville by Hornschuch in 1824)' has quasi-monopodial branching and perichaetia that match exactly those of the California specimens; most leaves, including the cauline, are long-lanceolate, with simple papillae over medially somewhat elongate laminal cells, as is the case with *Hymenostylium recurvirostrum*, but at least some leaves have the typical long-rectangular, apiculate leaves of much European *G. calcareum*. Most American specimens have elliptic leaves lacking an apiculus. Capsules of *G. calcareum* and *G. viridulum* have almost always enlarged, bulging exothelial cells, and when present prove a good marker for identification; the illustration of *G. aeruginosum* by Heyn and Herrnstadt (2004) exactly matches this concept of *G. calcareum*. An apparent isotype of *G. calcareum* at E differs from American material by the leaves being largely long-rectangular and apiculate, but some characteristic leaves are also present, and the perichaetial leaves are differentiated, while the exothelial cells are bulging. A toposytype specimen at B ('an den Nagelfluhwänden bei München an der Isar') is also *G. calcareum* in the present sense. Toposytype material from Salzburg or Munich ('628') at M have the gametophytes of *G. calcareum* but the capsules of *G. aeruginosum*, and may be a hybrid. Isotypes of *G. gracillimum* Nees & Hornsch., a synonym of *G. calcareum*, according to Whitehouse and Crundwell (1992), at E are actually *G. aeruginosum*, with loosely clasping, little modified, terminal perichaetia. The perigonia of *G. aeruginosum* have rather acute, somewhat modified bracts, and these should not be mistaken for the modified perichaetia of *G. calcareum*. When sterile, specimens in the west of North America may be identified as *G. calcareum* if the leaves are relatively short, and the distal leaf cells are very small (probably the smallest in the Pottiaceae), of the order of 5–6 μm wide, which is rare for *G. aeruginosum*. One may note, however, that the distal laminal cell widths of the isotype of *G. calcareum* average 7–9 μm , within the range for *G. aeruginosum*. This species is common in California, but of rare and scattered distribution elsewhere on the continent. The Missouri specimen has capsules similar to those of *G. aeruginosum*

but strongly differentiated perichaetial leaves with perigonial borne on short branches. The material from North Carolina was sterile but had typical perichaetia borne on short branches in fascicles from the apex of the plant. These plants are somewhat more robust than Californian representatives, with cauline leaves at the high end of the range of variation in length, and the adaxial epidermal cells of the costa were similar to those of *G. aeruginosum*. The strongly modified perichaetial leaves doubtless stimulated the original identification of these specimens as *Anoetangium euchloron* (Schwägr.) Mitt. (a blunt-leaved warm-temperate and tropical variant now a synonym of *A. aestivum*).

Representative specimens examined: U.S.A. California. Butte Co., *Schofield 23131* (UBC). Contra Costa Co., *M. A. Howe*, 28 February, 1896, c.fr. (NY). Fresno Co., *Shevock 14543* (MO). Lake Co., *Toren 8919* (MO), *Toren, Shevock & Dearing 7717a* (MO,CAS), *Toren 7536* (MO), *Toren 7064* (MO). Los Angeles Co., *McClatchie*, 17 March 1896, c.fr. (NY), *Habeeb 1307, 1362*, c.fr. (NY). Mendocino Co., *Steere*, 11 April 1953 (UBC). Monterey Co., *Norris 48537* (MO). Placer Co., *Whittemore 3527* (MO). Plumas Co., *Leiberg 5419*, c.fr. (NY). San Diego Co., *Steere 17506* (NY). San Francisco Co., *Toren 9461* (MO). Santa Barbara Co., *Toren 9462* (CAS). Santa Clara Co., *Schofield & Thomas 26445* (MO, UBC). Santa Cruz Co., *Kellman 927* (MO). Tuolumne Co., *Steere*, 1951 (NY). Trinity Co., *Duell & Duell 1730* (NY), *M. A. Howe 1152* (NY), *Showers 4163* (MO, SFSU). Tulare Co., *Shevock & Whitmarsh 17023* (CAS, MO), *Shevock 12958* (MO). Missouri. St. Louis Co., Lawrence, August 1903 (NY). North Carolina. Jackson Co., *Patterson T-54* (NY). Macon Co., *Sharp 36217* (NY). **Mexico.** Tamalipas, *Sharp 3505* (MO).

3. *Gymnostomum viridulum* Brid., *Bryologia Universa* 1: 66. 1826. Type: France, *Grateloup, s.n.*, 'Grateloupe, comm. DC' (B-holotype).

Gyroweisia luisieri C. Sérgio, *Bol. Soc. Portug. Cien. Natur.* 14: 82. 1972.

Plants dark green at least distally, usually forming a dense turf, occasionally loosely caespitose. *Cauline leaves* short-elliptic or ovate, occasionally long-elliptic, straight to weakly reflexed apically, 0.3–0.4(–0.6) mm, apex rounded to occasionally broadly acute, rarely apiculate, distal margins mostly unistratose, distal laminal cells 9–10 μm in width, 1 : 1; distal adaxial costal cells elongate, occasionally short-rectangular. *Specialized asexual reproduction* usually present, of obovoid gemmae of 4–6 cells in leaf axils. *Perichaetia* single on an elongate axis, terminating the axis, or lateral on a short branch; perichaetial leaves stiff or flexuose, long-ligulate to ovate-lanceolate, basal cells rectangular to rhomboid, smooth, distal laminal cells quadrate and strongly papillose or similar to the basal cells. *Capsule* short-cylindric, wide-mouthed, exothelial cells bulging, usually 30–40 μm wide.

Seepy, wet rock crevices but drying in summer and fall, 340–1500 m in New World. Distribution: California, Oregon; Eurasia; Africa.

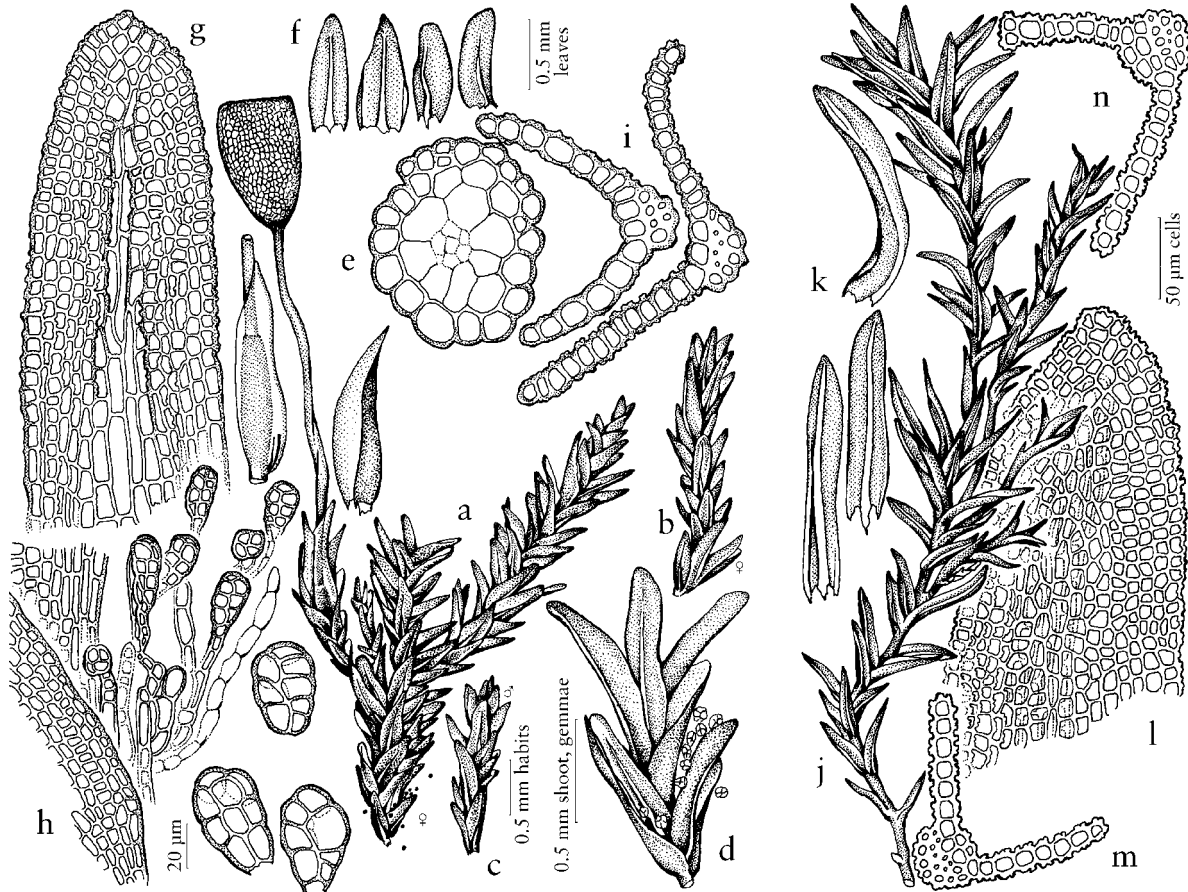


Figure 2. (a–i) *Gymnostomum viridulum*, California, Toren 328; (MO), (a) fruiting plant; (b) perichaetiate plant; (c) perigoniolate plant; (d) gemmiferous portion; (e) stem transverse section; (f) four cauline leaves; (g) leaf apex; (h) stalked gemmae; (i) transverse sections of leaves; (j–n) *G. aeruginosum*, California, Duell 1988/1; (MO), (j) habit; (k) three leaves; (l) leaf apex; (m, n) transverse sections of leaves.

In the New World, *Gymnostomum viridulum* is presently known only from California and Oregon in the U.S.A., found at low to middle elevations mostly in inland localities on various sedimentary, metamorphic, or metavolcanic rocks containing lime. It is best developed on large outcrops with overhangs and fissures from which water seeps during the wet winter season. In winter, globose colonies of cyanobacteria are often found growing among the tufts. During dry periods, the dense tufts shrink, producing a polygonal cracking pattern like dried clay. Bryophyte species often associated with *G. viridulum* are *Didymodon norrisii* R.H.Zander, *D. vinealis* (Brid.) R.H.Zander, *Anacolia menziesii* (Turn.) Par., *Weissia controversa* Hedw., and *Crossidium squamiferum* (Viv.) Jur. In at least one locality, *G. calcareum* and *G. viridulum* were found growing sympatrically (Toren 7717 and 7717a). Common associated vascular plants include *Aesculus californica*, *Juniperus californica*, *Keckiella corymbosa* and *Umbellularia californica*. Of some interest, at Hells Peak, Lake County, *G. viridulum* (Toren 328, 6866) grows with *Cheilanthes cooperae*, an obligate calciphilic fern endemic to California. The only sporophytes of *G. viridulum* found by the second author were from this site.

In Europe, *Gymnostomum viridulum* is fairly stenomorphic, with short-elliptic to long-ovate leaves that are widest at or just before the midleaf, and, unlike the California populations, the perichaetial leaves are generally similar to the cauline leaves; some specimens have few propagula or lack them entirely. The extremely similar *Gymnostomum mosis* of the eastern Mediterranean region supposedly differs in its distal leaf margins bistratose in patches and gemmae are absent (Heyn & Herrnstadt, 2004), but the unistratose *G. viridulum* may lack gemmae in some collections, and the type of *G. viridulum* is rarely bistratose in patches marginally. At least one other specimen seen (Greece, Zander 4083) has both distal leaf margins sometimes bistratose in patches and gemmae are present, as described for *G. viridulum* by Guerra (2004). Thus, differences between the two species are meager and perhaps not significant. Sporophytes and perichaetia are present, the latter with quite modified leaves, and usually lateral on short stalks, and one must beware of mixtures with *G. calcareum*, which has long-rectangular cauline leaves and bears no gemmae, although these may be introduced on the microscope slide through the mixed collection, or may occur on the protonema, but

not in the leaf axils. The gemmae of *G. viridulum* are diagnostic, but plants lacking gemmae but otherwise in extremely dense turf, plants dark green apically, with short-elliptic leaves, and generally with short, strongly differentiated perichaetia, may be at least provisionally assigned this name.

Didymodon brachyphyllus (Sull.) R.H.Zander, of western North America, phenocopies *G. viridulum* in its tight turf, ovate leaves with weak costa groove, costa subpercurrent, and at least the occasional presence of axillary gemmae, but it is KOH red (not vivid green) and there is a little hyaline window on the adaxial costal surface near the apex in larger leaves that is typical of the *D. vinealis* complex. Another phenocopy is *Anoetangium handelii* Schiffn., also known for California, which differs mainly in the cauline leaves recurved when wet (rather than strict) and deeply grooved along the costa. *Molendoa warburgii* (Crundw. & M.O.Hill) R.H.Zander of western Europe is similar but has short-lanceolate leaves with strongly papillose distal laminal cells. The unrelated species *Triquetrella papillata* (Hook. f. & Wilson) Broth. of Australia likewise has quasi-monopodial branching, with apparently both lateral and terminal perichaetia. The traditional characters used by recent European authors (e.g. Smith, 2004; Heyn & Herrnstadt, 2004) to distinguish *G. calcareum* from *G. aeruginosum* are on a spectrum and may be explained as associated with a wide range in plant size, but the sexual and capsule characters are fairly diagnostic.

Representative specimens examined: U.S.A. California. Butte Co., Norris 10630 (MO). Contra Costa Co., Shevock, Ertter, & Harris 24065 (CAS). Lake Co., Toren 8611 (MO). Humboldt Co., Schofield 28771 (UBC). Lake Co., Toren 328 (CAS, MO, SFSU). Santa Barbara Co., Toren & Shevock 9464 (CAS). Santa Clara Co., Steere & Sharp, 9 May, 1951 (MO), Schofield 29285 (UBC). Trinity Co., Toren 2995 (MO, SFSU). Tulare Co., Shevock 10142 (CAS). Oregon. Douglas Co., Wagner 7704 (MO, OSC). **U.K.:** E Cornwall, Long & Paton 7668 (MO). **Canary Islands.** La Palma, Long 7529 (MO). **Greece.** Island of Kos, Zander 4083 (MO). **Portugal.** Ophir, Sérgio 1319 (LISU—holotype of *Gyroweisia luisieri*).

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TAXONOMIC ADDITIONS AND CHANGES: *Gymnostomum aeruginosum* Sm. (syn. *Gymnostomum aeruginosum* var. *obscurum* J. Guerra).

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