

shape of the awns, and the ventricose capsule make the narrowly conceived *Racomitrium* readily distinguishable from its segregates.

SELECTED REFERENCES Tallis, J. H. 1959. Studies in the biology and ecology of *Rhacomitrium lanuginosum* Brid. J. Ecol. 47: 325–350. Tallis, J. H. 1964. Growth studies on *Rhacomitrium lanuginosum*. Bryologist 67: 417–422. Vitt, D. H. and C. Marsh. 1988. Population variation and phytogeography of *Racomitrium lanuginosum* and *R. pruinosum*. Beih. Nova Hedwigia 90: 235–260.

1. *Racomitrium lanuginosum* (Hedwig) Bridel, Muscol. Recent., suppl. 4: 79. 1818 [F]

Trichostomum lanuginosum
Hedwig, Sp. Musc. Frond., 107.
1801



Plants forming dark or grayish to yellowish green, yellowish to blackish brown tufts or patches, usually hoary when dry. **Stems** to 15 cm or more, radiculose at the base or not. **Leaves** crowded,

erect-appressed when dry, erectopatent when wet, straight to falcate-secund, linear-lanceolate, 3–5 × 0.6–0.9 mm; margins recurved to revolute for $\frac{1}{2}$ – $\frac{2}{3}$ the leaf length, entire proximally the echlorophyllose part formed by decurrencies from the awn; apices gradually tapering to a long and slender awn, not decurrent, canaliculate distally, concave to broadly carinate proximally, awn hyaline, densely papillose, broadly and evenly decurrent to $\frac{1}{4}$ – $\frac{1}{3}$ along the margins, with decurrencies consistently flat, erosodentate to nearly entire and short, to 30 μ m, sharp or blunt teeth, distinctly papillose throughout, spreading at a 40–90° angle; costa in tranverse-section rectangular to reniform in outline, strongly convex abaxially, 75–100 μ m wide basally; basal laminal cells long-rectangular, 40–90 × 7–8 μ m, strongly nodulose, forming a broad orange strip along the insertion; medial cells becoming long-rectangular to linear, 50–60 × 6–8 μ m wide; distal laminal cells short-rectangular, (10–)15–40 × 7–9 μ m. **Seta** 1–3 per perichaetium, brown to reddish brown, 3–7(–10) mm, erect, flexuose. **Capsule** brown, 1–1.7 mm, smooth, glistening; peristome teeth (300–)500–700(–900) μ m, reddish brown, arising from a low basal membrane, 2-fid almost to the base into filiform, terete, densely spiculate-papillose divisions. **Spores** 8–12 μ m.

Dry, exposed areas, mostly with high light intensity, acidic or seldom calciferous soil and rocks, boulders, cliffs, ledges, scree and in fellfields, polar tundra and tundra-like barrens in mountains, hummocks in peatland

and moorland, over raw earth of bog margins; low to high elevations (0–2300 m); Greenland; Alta., B.C., Man., Nfld. and Labr., N.W.T., N.S., Nunavut, Ont., Que., Yukon; Alaska, Calif., Idaho, Maine, Mont., N.H., Oreg., Wash.; Central America (Costa Rica); South America (Argentina, Chile, Colombia, Ecuador, Peru); Europe; arctic and temperate Asia (including Borneo, Java, New Guinea, Sumatra); South Africa; Atlantic Islands (Azores, Canary Islands, Falkland Islands, Gough Island, Iceland, Madeira, South Georgia, Tristan da Cunha); Indian Ocean Islands (Heard Island, Îles Crozet, Îles Kerguelen, Prince Edward Islands, Réunion); Pacific Islands (Hawaiian Islands, New Zealand); Australia; Antarctica (Deception Island).

Racomitrium lanuginosum is widely distributed throughout the Nearctic and Greenland, where it reaches the highest possible latitudes, becoming rare and scattered southwards. It usually occupies habitats of varying moisture regimes, but exhibits a tendency for growing in exposed, dry, and insolated situations. The often extensive and tumid patches of it found on rocks and soil are mostly hoary when dry. This is due to the very long hyaline awns that at once separate it from all other species of the broadly conceived *Racomitrium*. The shape of the hair-points is unique not only in the Grimmiaceae but among the mosses. *Niphotrichum* species often have a similar hoary appearance due to their long, papillose, hair-pointed leaves, but they differ from *R. lanuginosum* in having non-decurrent awns and tall, stout, conical papillae distributed over the leaf cell lumina, as well as large and often decurrent hyaline alar cells.

The laminal papillae of *Racomitrium lanuginosum* are identical to those of the genus *Codriophorus*, but species of that genus are usually readily distinguished by their mucous leaves. The only exception is *C. varius*, which often has pilose leaves but the awns are non-decurrent, smooth to faintly denticulate, and never papillose. Moreover, it has long-cylindric capsules, smooth setae, and very long, 1–1.8 mm peristome teeth, but in general sporophytes are produced infrequently in *R. lanuginosum*.

9. CODRIOPHORUS P. Beauvois, Mém. Soc. Linn. Paris 1: 445. 1822 • [Distorted Greek *kodon*, bell, and *phoras*, bearing, alluding to capsules with bell-shaped calyptrae]

Halina Bednarek-Ochyra

Ryszard Ochyra

Racomitrium subg. *Cataractarum* Vilhelm

Plants small, medium to large, mostly stiff and rigid, rarely pliant, robust to gracile, in green, yellow, olive, gray-green, brown to blackish mats. **Stems** creeping to ascending, repeatedly forked to sparsely fasciculately or pinnately branched, sometimes with short, tuft-like horizontal branchlets. **Leaves** lanceolate, ovate- or oblong-lanceolate, broadly ovate to broadly lingulate, elliptical to oblong-elliptical; margins 1-stratose to variously 2-stratose distally, mostly recurved on one or both sides, entire or erose-dentate to papillose-crenulate or crenate at apex; apices slenderly long-acuminate to rounded, rounded-obtuse to subacute, muticous or seldom with short to long awns, deeply concave to canaliculate-concave; costa single, reaching mid leaf to percurrent, entire or spurred and forked at tip, reniform to strongly flattened abaxially, 2–5-stratose in transverse section, situated in a shallow or deep, narrow- or wide-angled groove; laminal cells 1-stratose throughout to variously 2-stratose distally, elongate to linear throughout or isodiametric to shortly rectangular distally, with sinuose longitudinal walls becoming nodulose and porose with strongly incrassate walls in 2–3 rows at the base, mostly distinctly papillose with large, flat papillae covering longitudinal walls and major parts of the lumina leaving only a narrow groove in the center, occasionally more or less smooth. **Perichaetial leaves** differentiated, innermost elliptical to lingulate, hyaline throughout or chlorophyllose in the distal part. **Seta** dextrorse throughout or only with a single torsion to the right proximal to the urn and sinistrorse basally, erect, straight, smooth. **Capsule** brown, red-brown, or yellow-brown, straight, symmetric or nearly so, ovoid to long-cylindric; exothecial cells isodiametric to elongate, thick-walled; annulus 2–4-seriate; peristome teeth split to base or only to the middle into 2–3 terete, papillose branches. **Calyptra** distinctly verrucose to papillose distally. **Spores** spheric, finely papillose.

Species 15 (9 in the flora): North America, South America (Argentina, Chile, Colombia), Europe, arctic and temperate Asia, n Africa, Atlantic Islands (Azores, Canary Islands, Gough Island, Iceland, Madeira, South Georgia, Tristan da Cunha), Pacific Islands (Hawaiian Islands, Society Islands).

Codriophorus is primarily characterized by leaves that are distinctly papillose, with large flat papillae distributed on both abaxial and adaxial laminal surfaces, and over both the longitudinal walls and most of the lumina, leaving only a narrow slit in the middle. This disposition of the papillae gives a peculiar appearance to the transverse leaf sections. It consists of a regular pattern of distinct hollows over lumen centers separated by the large and equally thickened flat cuticular elevations over the walls and sides of the lumina. In addition, the calyptra is densely papillose towards the apex, the costa usually ends well before the leaf apex, and the seta is dextrorse (in species of subsect. *Fasciformes* twisted only once to the right proximally to the capsule and sinistrorse basally). The peculiar papillosity of the laminal cells is known otherwise only in the genus *Racomitrium*. That genus is distinguished by a strongly papillose seta sinistrorse on drying, slightly ventricose capsule, and presence of strongly papillose, long-decurrent, and erose-dentate awns.

SELECTED REFERENCES Bednarek-Ochyra, H. 2006. A Taxonomic Monograph of the Moss Genus *Codriophorus* P. Beauv. (Grimmiaceae). Cracow. Bednarek-Ochyra, H., D. Lamy, and R. Ochyra. 2001. A note on the moss genus *Codriophorus* P. Beauv. Cryptog. Bryol. Lichénol. 22: 105–111.

1. Distal laminal cells mostly short and isodiametric; costa robust and broad, usually more than 80 µm wide basally, 2–3-stratose distally and strongly convex abaxially, 3–6-layered in the basal part, lying at the bottom of a shallow, wide-angled groove; leaves lingulate to broadly ovate-lanceolate or lanceolate; plants absent short, lateral tuft-like branchlets 9a. *Codriophorus* sect. *Codriophorus*, p. 296
1. Laminal cells short-rectangular to linear throughout; costa fairly weak and narrow, usually less than 70 µm wide basally, 2-stratose and strongly flattened and weakly convex abaxially throughout or 3(-4)-layered and convex on the abaxial side in the proximal portion of the leaf (*C. varius*), situated at the bottom of a deep, narrow-angled furrow; leaves narrowly lanceolate to lanceolate; plants often with numerous lateral horizontal tuft-like branchlets 9b. *Codriophorus* sect. *Fascicularia*, p. 302

9a. CODRIOPHORUS P. Beauvois sect. CODRIOPHORUS

Racomitrium sect. *Papillosa* (Kindberg) Noguchi; *Trichostomum* sect. *Stenotrichum* Chevallier

Stem sparingly or freely irregularly, dichotomously or fasciculately branched, sometimes filiform and almost unbranched, absent short, lateral tuft-like branchlets. **Leaves** lingulate, elliptic, broadly ovate, ovate- or oblong-lanceolate to broadly or occasionally narrowly lanceolate; margins 1–2(-4)-stratose, recurved, reflexed, incurved or plane on both sides; apices narrowly to broadly rounded-obtuse or long acuminate to acute, muticous or very rarely shortly hyaline-tipped, entire or sharply to bluntly, remotely irregularly toothed, erose-dentate, sinuate to cristate in the upper $\frac{1}{5}$ – $\frac{1}{4}$; costa strong and broad, ceasing in mid leaf to subpercurrent, in transverse-section 2–4-stratose in the distal and medial parts, weakly to strongly convex, reniform, crescent-shaped to semi-terete abaxially, flat or convex on the adaxial side, in the basal part 3–6(-7)-layered, situated at the bottom of a shallow or deeper, usually wide-angled groove, lunate, reniform or rectangular and distinctly flattened, strongly convex on the abaxial side; basal marginal laminal cells not differentiated; distal laminal cells 1- to variously 2-stratose, irregularly rounded-quadrate, subquadrate, oval to rounded-hexagonal, strongly papillose to smooth, straight-walled in the distal part.

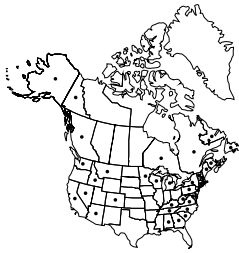
Species 9 (6 in the flora): North America, South America (Colombia), Eurasia, n Africa, Atlantic Islands (Azores, Canary Islands, Iceland, Madeira).

Members of sect. *Codriophorus* are recognized by their lingulate, broadly ovate to ovate- or oblong-lanceolate leaves, isodiametric and straight-walled distal laminal cells, and costa that is broad and robust, usually over 100 µm wide at the base. The costa is situated in a shallow, wide-angled groove and is mostly 2–4-stratose in the distal and medial parts, 3–6(-7)-stratose in the basal part, and anatomically strongly differentiated.

1. Laminal cells smooth or very slightly papillose on young leaves; leaf margins entire or with a few irregular teeth at the apex 5. *Codriophorus depressus*
1. Laminal cells distinctly papillose; leaf margins remotely irregularly toothed, erose-dentate, sinuate to cristate in the distal $\frac{1}{5}$ – $\frac{1}{4}$, if entire then broadly rounded-obtuse.
 2. Leaves lanceolate; apex irregularly bluntly erose-dentate; costa markedly convex and crescent-shaped abaxially 6. *Codriophorus ryszardii*
 2. Leaves lingulate, elliptical to broadly ovate or ovate-lanceolate; apex broadly rounded-obtuse to acute, irregularly dentate to entire.

- [3. Shifted to left margin.—Ed.]
3. Costa subpercurrent, entire and only shortly forked at the tip.
 4. Laminal cells strongly papillose, 1- or very rarely 2-stratose; leaves unbordered 1. *Codriophorus acicularis*
 4. Laminal cells indistinctly papillose over the cell walls, always variously 2-stratose in the distal part; leaves distinctly bordered with fleshy and broad limbidia 4. *Codriophorus norrisii*
 3. Costa extending $\frac{1}{2}$ – $\frac{3}{4}$ way up the leaf, distinctly spurred.
 5. Leaf apex broadly rounded, flat to subcucullate, always entire or sometimes sinuate to remotely bluntly erose-dentate 2. *Codriophorus mollis*
 5. Leaf apex broadly rounded-obtuse to subacute, often tubular, strongly dentate or very rarely subentire 3. *Codriophorus aduncoides*

1. *Codriophorus acicularis* (Hedwig) P. Beauvois, Mém. Soc. Linn, Paris 1: 445. 1823 (as *aciculare*)



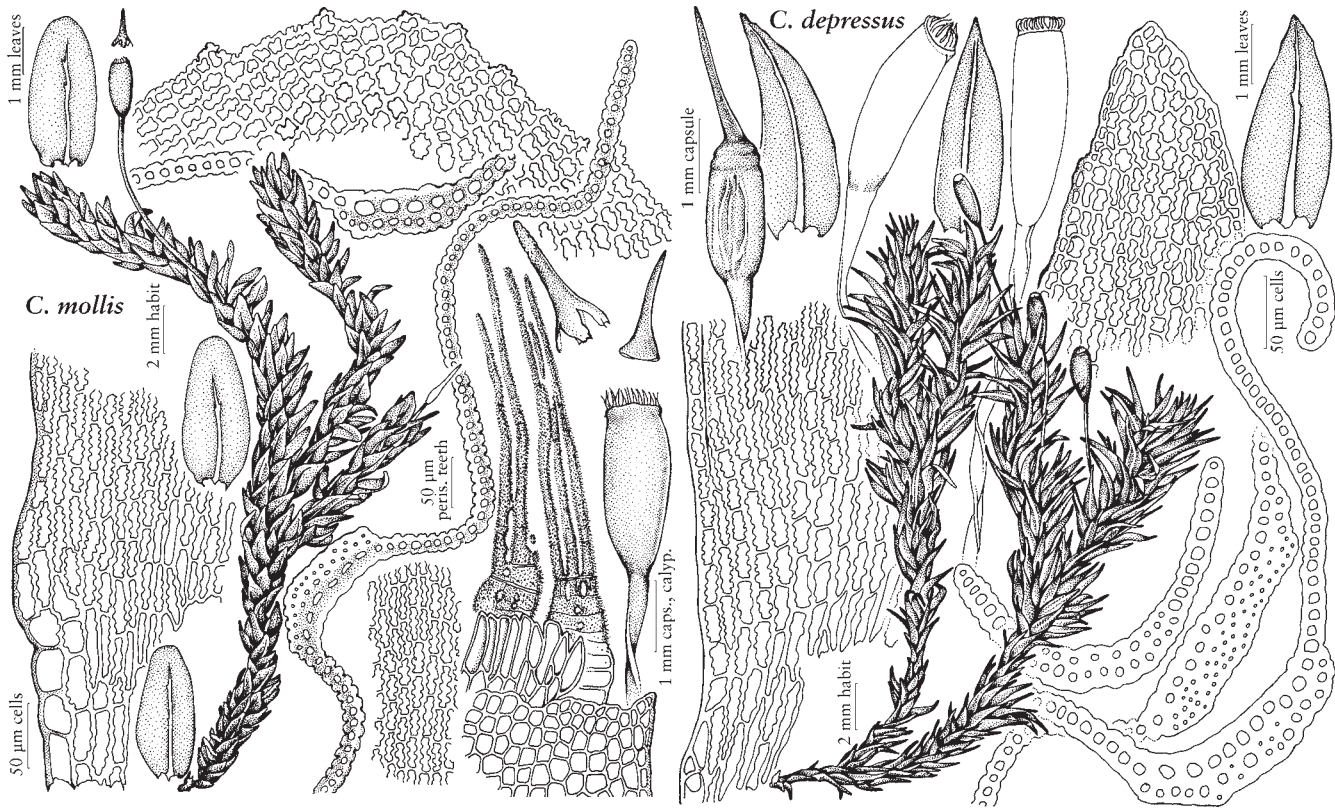
Dicranum aciculare Hedwig, Sp. Musc. Frond., 135. 1801; *Grimmia acicularis* (Hedwig) Müller Hal.; *G. nevii* Müller Hal.; *Racomitrium aciculare* (Hedwig) Bridel; *R. nevii* (Müller Hal.) S. Watson; *Trichostomum aciculare* (Hedwig) P. Beauvois

Plants mostly coarse, forming loose tufts or mats, dark or yellow- to olive green or yellow-, olive, rusty to blackish brown distally, brown, reddish or blackish brown proximally, sometimes black or brown throughout. **Stem** (1–)3–11(–15) cm, repeatedly forked or sparsely to copiously dichotomously or fasciculately branched. **Leaves** erect-appressed to imbricate, often secund on drying, erect-spreading on wetting, lingulate, elliptical, broadly ovate, ovate- or oblong-lanceolate to broadly lanceolate, (1.5–)2.2–2.9 (–3.2) × (0.8–)1–1.2 mm, margins recurved on both sides in the proximal half, plane, erect or somewhat inflexed in the distal part, 1-stratose, entire for about $\frac{3}{4}$ – $\frac{4}{5}$ of the distance to the apex, irregularly remotely, bluntly or sharply toothed, erose-dentate to sinuate at the apex; apices acute, subacute, rounded to broadly rounded-obtuse and mucous; costa subpercurrent, entire or shortly forked at tip, (60–)70–160(–180) μ m wide near the base; laminal cells 1- or very rarely 2-stratose distally, papillose or exceptionally smooth. **Inner perichaetial leaves** hyaline to yellowish hyaline, sometimes with chlorophyllose, thick-walled cells in the distal half or with a small group of chlorophyllose cells at the apex. **Seta** blackish or reddish brown, (1.8–)4–15(–17) mm. **Capsule** brown, ovoid, obloid to shortly cylindrical, (1–)1.5–2.8(–3.1) mm, smooth; peristome teeth lanceolate, (300–)350–450(–500) μ m, yellowish brown to dark reddish brown, densely low- or spiculate-papillose, 2-fid or tripartite down to the middle or two thirds of their length. **Spores** (10–)15–20 μ m.

Moist or wet, sometimes periodically dry, shaded acidic or rarely calciferous rocks, boulders, cliffs, slabs and blocks in stream beds or close to brooks and rivers periodically washed by wave action, in seasonal creeks and on lake shores, often permanently submerged in the rapids of streams and waterfalls; low to high elevations (0–3300 m); B.C., N.B., Nfld. and Labr., N.S., Ont., Que., Yukon; Ala., Alaska, Ariz., Calif., Colo., Conn., Ga., Idaho, Ky., Maine, Md., Mass., Mich., Minn., Mont., Nev., N.H., N.J., N.Y., N.C., Pa., R.I., S.C., Tenn., Vt., Va., Wash., W.Va., Wis.; Europe; temperate Asia; n Africa; Atlantic Islands (Azores, Canary Islands, Iceland, Madeira).

Codriophorus acicularis is a boreal-montane species, with a marked oceanic affiliation. It is bicentrically distributed in North America and, apart from *C. fascicularis*, is the most common species of the genus on the continent. In western North America it extends along coastal areas from the Aleutian Islands to central California. It recurs in the Rocky Mountains, with highly isolated stations in northern Colorado, where it reaches its highest altitude of 3292 m, and in southern Arizona. In eastern North America it has a continuous range from south-eastern Labrador to northern Georgia and Alabama, with two isolated stations on the Ozark Plateau of Arkansas and Oklahoma. In this part of the continent it reaches its highest elevation of 1525 m in the Great Smoky Mountains of Tennessee.

Codriophorus acicularis is central to a group of four species constituting the typical subsection of the genus; all occur in the flora area (H. Bednarek-Ochyra 2006). It is characterized by its percurrent costa that is unbranched or spurred and is situated at the bottom of a shallow, wide-angled, and open groove. In transverse section it is 2–3-stratose in the distal and medial parts, 3–6(–7)-layered in the basal part, and flattened to lunate and distinctly convex on the abaxial side. Moreover, the leaf margin is irregularly bluntly or sharply and coarsely dentate, erose-dentate, or only sinuate in the upper $\frac{1}{5}$ – $\frac{1}{4}$.



CODRIOPHORUS

2. *Codriophorus mollis* (Cardot) Bednarek-Ochyra & Ochyra in R. Ochyra et al., Cens. Cat. Polish Mosses, 141. 2003 [F]



Racomitrium molle Cardot, Bull. Herb. Boissier, sér. 2, 8: 333. 1908

Plants usually fairly soft, olivaceous, brown or yellow-rusty orange to blackish brown, sometimes dirty olive yellow, golden to blackish green distally, brown to blackish brown proximally, sometimes brown, blackish

brown to jet throughout. **Stems** 1–7(–10) cm tall. **Leaves** closely appressed and imbricate, erect, secund, erect-spreading to patent when dry, concave to cochleariform, broadly ovate, lingulate, elliptic, oblong or oblong-elliptic, (1.5–)2–2.5(–2.8) × 0.9–1.2 mm; margins 1-stratose, entire to subentire at the apex; apices very broadly rounded-obtuse and usually cucullate; costa ceasing at $\frac{1}{2}$ – $\frac{3}{4}$ of the way up the leaf, spurred and commonly forked at the apex, 75–100 µm wide at the base; laminal cells 1-stratose. **Inner perichaetial leaves** hyaline or with several thick-walled cells at the extreme apex or chlorophyllous throughout. **Seta** dark brown becoming black with age, fairly stout, 4–9 mm long. **Capsule** light to dark brown, obloid to shortly cylindrical,

1.2–2 × 0.7–0.8 mm; peristome teeth lanceolate, 400–425 µm long, reddish brown, densely spiculate-papillose throughout, divided nearly to the base into 2, or often imperfectly into 3 terete, rather unequal prongs. **Spores** (13–)17–20 µm.

Wet cliffs, dripping rocks, splashed or periodically flooded boulders, stones and outcrops in creek beds and the margins of watercourses, seepy sloping outcrops on roadsides and thin soil over moist rock ledges, in open and insolated as well as in diffusely lit and shaded sites on both acidic and basic substrates, scattered throughout coastal coniferous forests and in subalpine meadows and bogs; low to high elevations (0–2000 m); B.C.; Alaska, Calif., Wash.; South America (Colombia); e Asia.

Codriophorus mollis is a circum-north-Pacific species, ranging from Japan and Kamchatka across the Aleutian arc to northwestern North America, and with a highly disjunct locality in the paramo of the northern Andes of Colombia. In North America its main center of occurrence is in British Columbia, with some stations in northern California. It is closely related to *C. acicularis* but differs in the fairly soft texture of the plants, which are often almost unbranched and thread-like with a characteristic “calliergonoid” appearance owing to the imbricate foliage of broadly elliptical, lingulate, or ovate to oblong or oblong-elliptical leaves with very broadly rounded-obtuse, entire or faintly erose-dentate apices.

Moreover, the costa is slender, commonly spurred, and regularly forked at the apex, with one branch much longer and more slender, extending higher up the leaf than the other, usually reaching half or three quarters of the way up the leaf. The costa of *C. mollis* is similar to that in *C. aduncooides*, except for being more slender, 75–100 μm wide near the base in the former versus (80–)90–180 (–220) μm wide in the latter. Moreover, the leaf apex in *C. aduncooides* is often subacute and tubular owing to inflexed margins and is remotely bluntly or sharply dentate to erose-dentate.

3. *Codriophorus aduncooides* (Bednarek-Ochyra)

Bednarek-Ochyra & Ochyra in R. Ochyra et al., Cens. Cat. Polish Mosses, 140. 2003 [E]



Racomitrium aduncooides Bednarek-Ochyra, Fragm. Florist. Geobot. 44: 278, figs. 1–3. 1999

Plants rather stiff and rigid, in loose tufts or mats, olivaceous to golden brown, occasionally blackish brown. **Stems** (1–)3(–17) cm, irregularly forked. **Leaves** imbricate, erect to secund when

dry, ovate-elliptic, lingulate to oblong-lanceolate, (1.9–)2.3–3(–3.2) \times 0.8–1.1 mm; margins 1-stratose throughout, recurved on both sides in the proximal $\frac{3}{4}$, plane or often incurved at the apex giving it a subcucullate appearance; apices narrowly bluntly acute to broadly rounded, distantly bluntly or sharply erose-dentate to subentire, mucous; costa usually vanishing in mid leaf or sometimes extending $\frac{3}{4}$ of the way up the leaf, frequently spurred and forked at the tip, (80–)90–180 (–220) μm wide near the base; laminal cells 1-stratose throughout. **Seta** 8–11 mm. **Capsule** brown, obloid to shortly cylindric, 2–2.3 mm, peristome teeth 480–520 μm , orange- to yellow-brown, split nearly to the base into 2 filiform, densely papillose branches. **Spores** 14–17 μm .

Wet acidic rocks and boulders in or close to streams, damp and wet cliffs, often submerged in swiftly flowing brooks or on rocks in waterfalls and cascades; moderate to high elevations (300–2100 m); Conn., Ky., Maine, N.H., N.J., N.Y., N.C., Pa., Tenn., Vt., Va., W.Va.

Codriophorus aduncooides is a montane, hydrophilous, acidophilous moss that can tolerate periodic desiccation. It is restricted to the Appalachian Mountains, ranging from western Maine to Tennessee and North Carolina. *Codriophorus aduncooides* has only recently been recognized as a species, being segregated from the common and protean *C. acicularis*. The two species share similar leaf shape and areolation as well as identical ecological predilections, but *C. aduncooides* is well-defined and easy to distinguish by the structure of the costa. It is

generally shorter and vanishes in mid leaf or extends at most to three quarters of the way up the leaf. It is distinctly spurred on both sides in the distal portion and is mostly forked at the apex. Additionally, the leaves are usually falcate-secund and the leaf apex is often tubular to subcucullate owing to the inflexed margins.

4. *Codriophorus norrisii* (Bednarek-Ochyra & Ochyra)

Bednarek-Ochyra & Ochyra in R. Ochyra et al., Cens. Cat. Polish Mosses, 141. 2003 [C] [E]



Racomitrium norrisii Bednarek-Ochyra & Ochyra, Ann. Bot. Fenn. 37: 236, figs. 1–3. 2000

Plants mostly small to moderately sized, stiff, loosely tufted, olivaceous distally, blackish brown proximally. **Stems** (1.5–)2–3(–3.5) cm long. **Leaves** appressed, closely imbricate, erect, lingulate to

oblong-lanceolate, (1.7–)2.0–2.5(–3.0) \times 0.7–0.8(–0.9) mm; margins 2(–4)-stratose throughout, variously recurved on both sides in the proximal $\frac{1}{2}$, plane distally, entire basally, bluntly erose-dentate at the extreme apex or sometimes down the margin in the upper one fourth, occasionally subentire, bordered from nearly the base by (1–)2–10(–13) rows of cells in 2(–4) layers; apices acute to long-acuminate, less often rounded-obtuse and subacute; costa subpercurrent, entire and only shortly forked at the tip, 70–90(–120) μm wide; laminal cells 1-stratose throughout (except for the margins) to variously 2-stratose near the apex and with 2-stratose streaks in the proximal part, without or with inconspicuous papillae over the cell walls. **Inner perichaetial leaves** sheathing, yellowish brown to hyaline proximally, chlorophyllose in the upper one third and, with areolation similar to that of the vegetative leaves and with frequent 2-stratose patches at the margin. **Seta** brown, 4–4.2 mm. **Capsule** obloid to shortly cylindric, 1.5–2 mm; peristome teeth 340–420 μm , orange-brown, irregularly split to the middle or slightly below into 2–3 filiform prongs, densely papillose. **Spores** 15–20 μm .

Wet granite stones, boulders, and rockslabs in and at banks of streams and rivers, usually subject to temporary inundation or submerged; moderate elevations (500–1600 m); of conservation concern; Calif., Idaho.

Codriophorus norrisii is a relatively rare montane species. It is closely related to the widespread and common *C. acicularis*, with which it shares the lingulate leaves with erose-dentate margins at the apex and similar affiliation to aquatic habitats. It is generally a smaller and fairly slender plant, with most leaves long-acuminate to acute. The leaves have distinct marginal thickenings that extend from the base to the apex and are separated from the costa by 1-stratose laminae, even at the extreme

apex; rarely do they merge imperceptibly with 2-stratose laminae. Moreover, papillae are absent on older leaves or are narrow and situated strictly over the cell walls. The innermost perichaetial bracts are strongly concave, yellowish brown to hyaline in the basal two thirds, with a lax areolation of thin-walled cells, whereas in the distal one third the cells are chlorophyllose and similar to those in the vegetative leaves, usually with 2-stratose patches in 1–3 rows at the margins. In contrast, the plants of *C. acicularis* are larger and coarse, the leaves are usually rounded-obtuse at the apex, and the leaf laminae are 1-stratose in North American specimens, except for a few collections from California (e.g., *Shevock & York 18322*, CAS, KRAM). However, the latter are at once distinct by having very large, flat papillae that cover almost the entire lumina of the cells, leaving only a narrow groove over the cell center. Additionally, the innermost perichaetial leaves in *C. acicularis* are hyaline throughout, occasionally with some chlorophyllose cells at the extreme apex. The 2-stratose distal laminal cells of *C. norrisii* may resemble those of *C. depressus*, which, however, has broadly ovate-lanceolate to broadly ovate and deeply concave leaves, mostly smooth or indistinctly papillose laminal cells, and a very broad costa that is strongly flattened abaxially and has 9–15 enlarged adaxial epidermal cells in the basal part.

5. *Codriophorus depressus* (Lesquereux) Bednarek-Ochyra & Ochyra in R. Ochyra et al., *Cens. Cat. Polish Mosses*, 140. 2003 [E][F]



Racomitrium depressum
Lesquereux, *Mem. Calif. Acad. Sci.*
1: 14. 1868

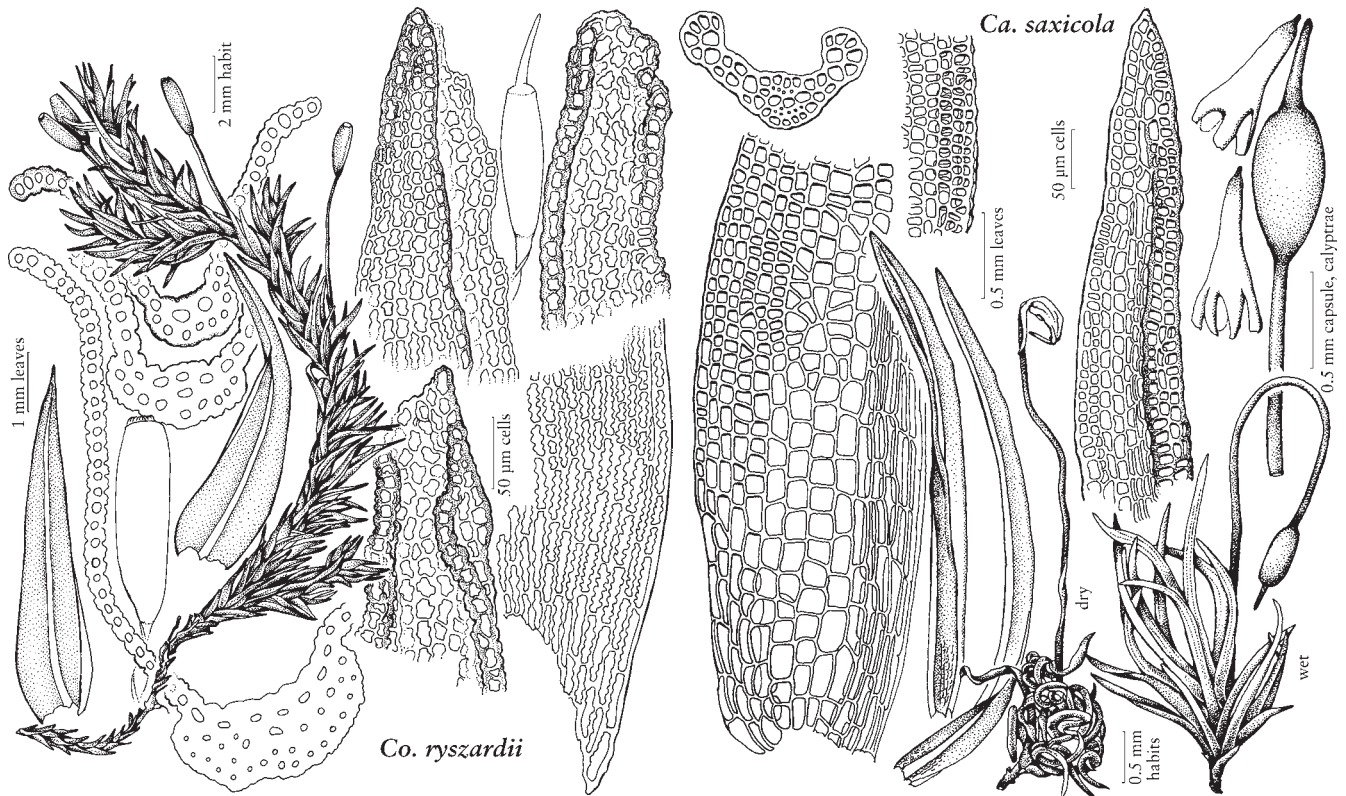
Plants large and rigid, forming extensive patches or loosely caespitose, olive or yellowish green, olivaceous, olive, golden, or rufous brown to blackish green distally, brown to blackish brown

proximally, sometimes dark blackish green to black throughout. **Stems** (2–)4–10(–13) cm long, tough. **Leaves** oblong- or ovate-lanceolate to broadly ovate, (2.1–)3–4.5(–5) × (0.8–)1–1.3(–1.5) mm; margins 1- or 2-stratose distally in several rows of cells, entire or sometimes sinuate or with a few blunt, irregular teeth at the apex; apices acute or obtuse; costa subpercurrent, (80–)100–200 μm wide at the base; laminal cells 1-stratose throughout or entirely to partially 2-stratose in the distal part, smooth or very slightly papillose on young leaves.

Inner perichaetial leaves yellowish hyaline throughout. **Seta** brown, 4.5–7 mm. **Capsule** brown to reddish brown, symmetric or slightly curved and gibbous, obloid to cylindric, 1.8–3 mm, peristome teeth, lanceolate, 350–500 μm high, reddish or yellowish brown, finely papillose to nearly smooth basally, densely low-papillose distally, deeply 2-fid or tripartite down for two thirds of their length. **Spores** (10–)12–15(–17) μm.

Semi-aquatic on granitic rocks or soil; moderate to high elevations (1300–2800 m); Calif., Nev., Oreg.

Codriophorus depressus is a semi-aquatic saxicole growing directly attached to or on soil over granite boulders, walls, stones and slabs along the banks of intermittent flowing watercourses or in stream beds. It is often submerged in swiftly flowing water in the rapids of intermittent streams or in cascading streamlets, or on dripping rocks and seeps over exposed granite rock terraces during snowmelt that then become dry by mid-summer. It is most often found in shaded or diffusely lit sites, rarely in open, permanently or seasonally dry habitats, throughout subalpine mixed coniferous forests, and it is restricted in its distribution to California except for a single record in the border area of adjacent Nevada at Lake Tahoe and southern Oregon (Jackson County). The species is primarily characterized by the costa that is exceptionally broad, strongly flattened and weakly convex on the abaxial side, and U-shaped adaxially in the distal part, the leaves that are broadly concave to broadly canaliculate, as well as laminal cells that are smooth or only very slightly papillose. *Codriophorus depressus* is superficially similar to *C. acicularis* and *C. norrisii*, but the leaves in those two species are broadly lingulate, acute to broadly rounded, and usually distinctly dentate or erose-dentate at the apex, and the costa is generally narrower and crescent-shaped on the abaxial side. Particularly reliable for distinguishing *C. acicularis* and *C. norrisii* are the prominently papillose laminal cells, which sharply contrast with the smooth or only finely roughened cells in *C. depressus*. Moreover, *C. norrisii* has distinctly limbate leaves almost all around, and the innermost perichaetial leaves are chlorophyllous in the distal third. *Codriophorus depressus* is more likely to be confused with *Bucklandiella pacifica*, which, however, has smaller leaves, less than 3 × 1 mm, and its costae are narrower, less than 120 μm, distinctly narrowly canaliculate distally and lying at the bottom of a deep and narrow-angled groove, partly enclosed in the basal part. Moreover, *B. pacifica* is a lowland species, whereas *C. depressus* is a montane moss.



CODRIOPHORUS • CAMPYLOSTELIUM

6. *Codriophorus ryszardii* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in R. Ochyra et al., Cens. Cat. Polish Mosses, 141. 2003 [E] [F]



Racomitrium ryszardii Bednarek-Ochyra, Cryptog. Bryol. Lichénol. 21: 276, figs. 1–3. 2000

Plants medium-sized to large, in loose, extensive tufts or mats, dull, green, yellow-brownish or olive to green-brown. **Stems** (1)–2–7 cm or occasionally up to 10 cm long, prostrate to ascending, irregularly

sparsely branched, usually radiculose at base. **Leaves** lanceolate to linear-lanceolate, (2.8–)3.2–4.0(–4.2) × 0.8–1(–1.1) mm; margins 1-stratose throughout, recurved on both sides to about $\frac{3}{4}$ – $\frac{7}{8}$ of way up the leaf; apices slenderly long acuminate, obtuse to subacute, irregularly bluntly erose-dentate, cristate to papillose-crenulate, rarely entire at the extreme apex; costa subpercurrent, (80–)90–120(–135) µm wide; laminal cells 1-stratose throughout. **Seta** brown, (4.5–)5.5–7.5(–9) mm. **Capsule** brown, cylindric, (2–)2.3–3(–3.2) mm, smooth; peristome teeth 500–650 µm, dark yellow to orange-brown, regularly 2-fid to the base, densely papillose with tall, spiculate papillae. **Spores** 10–16 µm.

Moist or wet, seldom dry, shaded or exposed granite, basalt and sandstone, rarely limestone rock outcrops, boulders and cliff faces in stream beds and on stream or lake banks throughout the coastal coniferous forest; low to high elevations (0–2200 m); B.C.; Alaska, Oreg., Wash.

Codriophorus ryszardii ranges from Kodiak Island southwards to the Olympic Mountains and Cascade Range of Washington and northern Oregon. The species was recognized as a distinct taxon only recently by Bednarek-Ochyra, who showed that the western North American specimens determined as *Racomitrium aquaticum* (Schrad.) Bridel (W. B. Schofield 1968, 1976; E. Lawton 1971) had nothing to do with that European endemic and represented a new species. Although there are some similarities in the structure of the costa, *C. ryszardii* is immediately distinct in having lanceolate to linear-lanceolate leaves, 3.2–4 mm. They are narrowly long acuminate and end with an obtuse or subacute apex that is most often bluntly erose-dentate, giving it a cristate appearance, and only seldom is the leaf apex entire. Moreover, its leaf margins are recurved to $\frac{3}{4}$ – $\frac{7}{8}$ of the leaf length, costae are often bluntly winged abaxially in the distal portion, laminal cells are entirely 1-stratose, and the supra-alar cells are not differentiated from the adjacent laminal cells and do not form basal marginal borders. Additionally, the peristome teeth are longer,

500–650 µm, and they are densely papillose with needle-like papillae. The leaves of *C. aquaticus* are shorter, 2.5–3 mm, broadly lanceolate and more shortly acuminate into an obtuse and always entire, never erose-dentate or cristate apex. Moreover, the leaf margins are recurved to $1/2$ – $3/4$ of the leaf length, costae are symmetric and never winged abaxially, laminal cells are sometimes 2-stratose

distally, the supra-alar cells are quadrate to short-rectangular with relatively thick, smooth to slightly sinuose walls forming short but usually distinct, hyaline to yellowish-hyaline but otherwise pellucid marginal borders, and the peristome teeth are shorter, to 450 µm, and they are only finely papillose.

9b. CODRIOPHORUS sect. FASCICULARIA (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in R. Ochyra et al., Cens. Cat. Polish Mosses, 140. 2003.

Racomitrium sect. *Fascicularia* Bednarek-Ochyra, Fragm. Florist. Geobot., Ser. Polon. 2: 130. 1995

Stems often subpinnately branched with numerous short, tuft-like, lateral, horizontal branchlets, giving the plants a nodose appearance. **Leaves** ovate-lanceolate, narrowly lanceolate to linear-lanceolate, from an ovate, oblong- or ovate-lanceolate, not or distinctly plicate base, gradually short- or long-acuminate, often with a long, subulate, canaliculate-concave, straight or sometimes wavy to serpentine acumen; margins 1-stratose, recurved to revolute on both sides; apices muticous, acute, subacute to narrowly rounded-obtuse, entire, erose-dentate or denticulate-cristate, epilose or terminated with a hyaline, denticulate awn; costa narrow, vanishing in mid leaf to subpercurrent or percurrent, in the proximal part lying at the bottom of a deep, wide- or narrow-angled furrow, open or partly enclosed by the strongly infolded leaf base, in transverse section 2-stratose throughout, with occasional 3-stratose spots near the base or 2-stratose in the distal and 3–4-stratose in the proximal parts, flattened or convex on the ventral side, not prominently convex, lunate or flattened on the abaxial side, with cells in the abaxial and adaxial rows of similar size and shape or with 1–2 abaxial rows composed of small stereid cells in the proximal $1/2$ or at the extreme base; laminal cells 1-stratose, short- or long-rectangular to linear, thick- and sinuose-walled throughout; basal marginal border differentiated, pellucid; distal laminal cells exceptionally variously 2-stratose and isodiametric.

Species 6 (3 in the flora): North America, South America (Argentina, Chile), Europe, arctic and temperate Asia, Atlantic Islands (Azores, Gough Island, Iceland, South Georgia, Tristan da Cunha), Pacific Islands (Hawaiian Islands, Society Islands).

Members of sect. *Fascicularia* are recognized by their narrowly lanceolate to linear- or ovate-lanceolate leaves, short-rectangular to linear laminal cells, and peculiar anatomical structure of the costa, which is narrow, usually less than 80 µm wide at the base, and mostly 2-stratose throughout and composed of undifferentiated cells in both adaxial and abaxial rows. Only in the highly isolated *C. varius* is the costa broader, to 110 µm near the base, and 3–4-stratose in the proximal half, but in all species of the section it is lying at the base of a deep and narrow-angled groove that is often partly enclosed by the strongly folded leaf base.

1. Costa 3(–4)-stratose, lunate and distinctly convex on the abaxial side, 75–135 µm wide proximally; leaves usually piliferous, if muticous then entire; peristome teeth 1.0–1.8 mm 9. *Codriophorus varius*
1. Costa 2-stratose throughout except the extreme base, flattened and weakly convex on the abaxial side, less than 70 µm wide proximally; leaves muticous; peristome teeth less than 1 mm.

[2. Shifted to left margin.—Ed.]

2. Costa extending $\frac{3}{4}$ way up the leaf to subpercurrent; leaf apex entire; leaf acumen straight 7. *Codriophorus fascicularis*
2. Costa ending in mid leaf or only slightly distally; leaf apex erose-dentate; leaf acumen serpentine, strongly wavy 8. *Codriophorus corrugatus*

7. *Codriophorus fascicularis* (Hedwig) Bednarek-Ochyra & Ochyra in R. Ochyra et al., Cens. Cat. Polish Mosses, 141. 2003



Trichostomum fasciculare Hedwig, Sp. Musc. Frond., 110. 1801;
Racomitrium canescens subsp. *delamarei* Renault & Cardot;
R. delamarei (Renault & Cardot) Renault & Cardot; *R. fasciculare* (Hedwig) Bridel; *R. fasciculare* var. *haplocladon* Kindberg; *R. fasciculare* var. *nigricans* Warnstorff;

R. microcarpon var. *palmeri* Kindberg; *R. palmeri* (Kindberg) Kindberg; *R. tenuinerve* Kindberg

Plants fairly coarse to slender, densely to loosely caespitose or forming extensive patches or mats, dull, yellow, yellow-to olive brown, yellow-green to green, brown to blackish brown distally, brown to blackish brown proximally, sometimes brown or black throughout. **Stems** (1–)4–10 or, sometimes, as much as 20 cm, often with short, tuft-like, lateral branchlets. **Leaves** straight to somewhat curved, narrowly lanceolate to linear- or ovate-lanceolate, (1.5–)2.2–3.6(–4) × 0.5–1(–1.5) mm wide; margins entire throughout; apices gradually tapering to a straight acumen, acute to narrowly rounded-obtuse, entire distally; costa extending $(\frac{2}{3}-\frac{3}{4}-\frac{5}{6})$ of the leaf length, (40–)50–70(–80) μm wide at the base, 2-stratose throughout; laminal cells long rectangular, (10–)20–60(–70) × (5–)7–8(–10) μm. **Inner perichaetial leaves** oblong-lanceolate to elliptic, yellowish hyaline throughout. **Seta** reddish to blackish brown, (2–)3–8(–11) mm. **Capsule** brown, ellipsoid, obloid to cylindric, (1–)1.2–2.5(–3.1) mm, smooth, lustrous, peristome teeth 550–600(–800) μm, reddish brown, densely spiculate-papillose, split nearly to the base into to 2 filiform prongs, with a low basal membrane. **Spores** 12–15(–17) μm.

Exposed or protected, moist granite, basalt, gneiss, and sandstone, boulders, stones, cliffs, and rock faces and outcrops in or close to streams, creeks, brooks and lakes, often in sites periodically submerged or splashed with water, in seepage and melt-water runnels,

occasionally bark at tree bases, logs in water and shingle roofs; low to high elevations (0–4100 m); Greenland; St. Pierre and Miquelon; Alta., B.C., N.B., Nfld. and Labr., N.W.T., N.S., Ont., Que., Yukon; Alaska, Colo., Idaho, Maine, Mich., Minn., Mont., N.H., N.Y., Oreg., Vt., Wash.; Eurasia; Atlantic Islands (Azores, Iceland); Pacific Islands (Society Islands).

Codriophorus fascicularis is one of the most common species of the genus, with two centers of distribution. It is more frequent and abundant in western North America, extending from the Aleutian Islands and western Alaska southwards to northern Oregon, with highly isolated stations in Colorado, where it reaches its highest altitude of about 4100 m in North America. In the eastern part of the continent it ranges from Labrador to the Adirondack Mountains of New York. It is the only species of the genus in North America that occasionally penetrates into the Arctic. It barely reaches beyond the Arctic Circle in the Baird Mountains in Alaska and has once been recorded on Baffin Island slightly below the Arctic Circle. The species is common and abundant in the southern parts of East and West Greenland, and in the latter region it crosses the Arctic Circle, extending to ca. 70° N on Disko Island.

Codriophorus fascicularis is at the core of a complex of four closely related species that all occur in East Asia and constitute subsect. *Fasciformes* within sect. *Fascicularia* (H. Bednarek-Ochyra 2006). In the flora area that subsection comprises also *C. corrugatus*. *Codriophorus fascicularis* is characterized by its costa that extends $\frac{3}{4}-\frac{5}{6}$ or very rarely only $\frac{2}{3}$ of the way up the leaf and is spurred or forked at the apex only. The costa is situated at the bottom of a moderately deep, wide-to narrow-angled and open or partly closed channel, and in transverse section it is flat on the adaxial side and flattened to somewhat curved abaxially. In addition, the leaf margins are entire all around including the apex, and the basal marginal cells form a distinct pellucid border consisting of 5–18 cells. It is likely to be mistaken for *C. corrugatus* and epilose ecads of *C. varius*; the characters discriminating them are discussed under those species.

8. *Codriophorus corrugatus* Bednarek-Ochyra,
Bryologist 107: 377, figs. 1–77. 2004 [C]



Plants moderately sized, growing in dense turfs, dull, olivaceous distally, brown proximally. **Stems** 3–4 cm. **Leaves** ovate-lanceolate to narrowly lanceolate, 2.5–3 × 0.7–0.8 mm; margins entire proximally, cristate or papillose-crenulate at the apex, variously infolded in the acumen; apices

shortly acuminate, with a fine, corrugate and wavy acumen, acute; costa single but often laterally spurred distally, disappearing in mid leaf, 40–60 μm wide near the base, 2-stratose throughout, with 6–9 large adaxial epidermal cells; basal and medial cells long and linear, up to 150 μm, distal cells rectangular to long-rectangular, (25–)30–80 × 6–8 μm. **Seta** dark brown, 4–8 mm. **Capsule** brown, obloid to cylindric, 1.5–2 mm; peristome teeth 640–760 μm, yellow- or orange-brown, split to the base into 2 filiform prongs, densely papillose. **Spores** 14–20 μm.

Birch-spruce forests; elevation unknown; of conservation concern; Alaska; arctic and temperate Asia.

Codriophorus corrugatus is an east-Asian northwestern North American disjunct boreal-temperate-montane species. It has only once been collected in North America, in southern Alaska at Dyer's Lake between Anchorage and Fairbanks. The species is widely distributed but scattered in temperate eastern Asia. It is readily distinguished from all other species of the genus by its peculiar leaf acumen and costa. The snake-like leaf acumen is corrugate or ruffled in the distal part and erose-dentate, cristate, or papillose-crenulate at the apex. The short costa typically extends to the mid leaf or only a little more distally in some leaves and is often laterally spurred or forked at the apex. The species may be mistaken for *C. fascicularis* but in that species the costa extends to $\frac{3}{4}$ or further up the leaf and is entire throughout. Also, the leaf apex in *C. fascicularis* is entire, whereas in *C. corrugatus* it is erose-dentate or cristate. The peristome teeth in *C. fascicularis* are generally shorter, up to 600 μm, whereas *C. corrugatus* has longer teeth, 640–760(–950) μm.

9. *Codriophorus varius* (Mitten) Bednarek-Ochyra & Ochyra in R. Ochyra et al., Cens. Cat. Polish Mosses, 141. 2003 [E]



Grimmia varia Mitten, J. Linn. Soc., Bot. 8: 21. 1865; *G. speciosa* Müller Hal.; *Racomitrium canescens* var. *lutescens* Lesquereux & James; *R. oregonum* Renaud & Cardot; *R. speciosum* (Müller Hal.) Kindberg; *R. varium* (Mitten) A. Jaeger

Plants mostly robust and coarse, loosely tufted or forming intricate patches, yellow, green, yellow-, grayish or olive green distally, brown to blackish brown proximally. **Stems** 5–12 cm or sometimes to 20 cm, sometimes with short, lateral tuft-like branchlets. **Leaves** ovate-lanceolate to lanceolate, from an ovate, plicate base, (2.5–)3–3.7(–4) × 1–1.2(–1.5) mm; margins entire; apices slenderly or broadly acuminate, piliferous or mucous, subacute to narrowly rounded-obtuse, awns hyaline, 0.1–0.75(–1.2) mm, erect to recurved, flattened, finely and irregularly spinulose-denticulate or denticulate; costa percurrent or subpercurrent, 75–100(–110) μm wide at the base, in transverse section 2-stratose in the distal portion, 3–4-stratose in the proximal part; basal laminal cells long-rectangular, (20–)35–60(–75) × 5–8 μm; medial laminal cells becoming elongate, (20–)30–45(–50) × 7–8 μm; distal laminal cells mostly short-rectangular, (8–)13–20(–30) × 7–8 μm. **Inner perichaetial leaves** oblong-lanceolate, longitudinally plicate, 2.2–2.5 × 0.9–1 mm, hyaline. **Seta** dark brown, (0.6–)1.2–2(–2.2) cm. **Capsule** brown or yellowish brown, lustrous, cylindric, (2.5–)3–4.2 × 0.8–1 mm, smooth or somewhat sulcate when old and empty; peristome teeth dark reddish brown, 1–1.8 mm long, faintly papillose to nearly smooth, regularly split nearly to the base into 2, thread-like, terete, equal or unequal branches. **Spores** 12–15 μm.

Acidic to basic rocks, such as limestone, granite, diorite, basalt, serpentine, schist, and sandstone, concrete walls of buildings, sandy or clayey soil, humus, tree trunks and bases, in a wide range of habitats, from protected, shaded and damp or wet to open, fully or diffusely lit and dry in coastal mixed and coniferous forests, woodlands, grasslands, forest glades, also on the banks of streams, creeks and lakes and by waterfalls, usually in places above the flood line, but sometimes in occasionally submerged sites or on pockets of sand in stream beds, outcrops in fens, partially drained bogs, seepage, roadcuts and earthy roadside banks; low to high elevations (0–1700 m); B.C.; Calif., Idaho, Oreg., Wash.

Codriophorus varius occurs predominantly at low elevations. It is widespread and locally common and abundant in coastal areas from the Queen Charlotte Islands southwards to central California, and only once recorded in the Rocky Mountains of northern Idaho. It is one of the most distinctive species of the genus, easily recognized by leaves usually with an awn, long cylindrical capsules, and very long peristome teeth, 1–1.8 mm, the longest in the genus, that are split to the base into two filiform branches. Sporophytes are usually produced in great profusion and enable easy identification. Epilose ecads of *C. varius* are likely to be mistaken for robust and coarse phenotypes of *C. fascicularis*, especially when

sterile, but the species is distinct in having leaves plicate at the base, with shorter distal laminal cells, and a costa 3-stratose in transverse-section in the proximal half. Some specimens have occasionally been mistaken for *Bucklandiella pacifica*, which, however, has entirely smooth laminal cells that are mostly rounded-quadrate distally. The leaves of *B. pacifica* are narrowly canaliculate in the distal half, and generally smaller, less than 3 mm, with the margins broadly recurved to $2/3$ – $3/4$ of the leaf length on one side and more narrowly recurved to $1/2$ the leaf length or plane on the other side. In addition, the capsules and peristome teeth are much shorter in the latter species.