22. DICRANACEAE Schimper

Robert R. Ireland Jr.

Plants small to large, often in dense tufts. **Stems** erect, simple or dichotomously to irregularly branched, usually with central strand, often densely radiculose, tips occasionally deciduous. **Leaves** in several rows around the stem, erect or secund, often falcate-secund, sometimes crispate, short- to long-lanceolate, whole leaves or their tips sometimes deciduous; costa single, usually strong, percurrent to excurrent, sometimes ending in a short to long hyaline awn, smooth, ridged or lamellose on abaxial surface, rhizoids occasionally on adaxial or abaxial surface near leaf base; laminal cells smooth or sometimes distal cells mammillose or papillose on one or both sides, papillae rarely forked, or toothed by projecting cell ends, pitted or nonpitted; proximal cells elongate, often differentiated in alar region, sometimes undifferentiated. **Specialized asexual reproduction** absent or occasionally present as brood leaves, microphyllous branches, borne in axils of distal leaves or as rhizoidal tubers. **Sexual condition** autoicous, dioicous or pseudomonoicous. **Seta** solitary or several per perichaetium, elongate, usually straight, sometimes flexuose or cygneous. **Capsule** exserted, erect, inclined, or sometimes curved, cylindrical or ovoid, smooth, ridged, furrowed or irregularly wrinkled, sometimes strumose; stomata present or absent, superficial; annulus present or absent, often compound, deciduous or persistent; operculum conic or obliquely rostrate from a conic base; peristome single, usually of 16 lanceolate teeth, deeply divided into 2 or rarely 3 divisions, usually vertically striolate or pitted-striolate proximally, papillose distally. **Calyptra** cucullate, smooth, naked, sometimes fringed at base, usually covering most of capsule, fugacious. **Spores** mostly spheric, smooth to papillose.

Genera 50–52, species ca. 900 (17 genera, 90 species in the flora): worldwide.

Distinctive characters of this large acrocarpous family include the erect, often tomentose stems; mostly narrow, lanceolate, occasionally falcate or falcate-secund leaves, with a single, narrow to broad costa, with or without rhizoids at the base, sometimes ending in a hyaline, occasionally toothed apex, costa in cross section with or without stereid bands, leaf cells usually smooth, sometimes mammillose, or rarely with a single papilla on one or both sides, papillae rarely forked, asexual propagation by specialized deciduous branches, deciduous leaves or leaf apices, rarely rhizoidal tubers; sporophytes usually solitary or rarely clustered, setae mostly elongate, straight or rarely flexuose or cygneous, capsule cylindric to ovoid, erect to horizontal, smooth or ribbed, sometimes strumose, operculum usually obliquely rostrate, peristome single, with 16 teeth often divided 1/2 way to the base, usually striolate or pitted-striolate proximally, papillose distally.

SELECTED REFERENCES Müller, P. and J.-P. Frahm. 1987. A review of the Paraleucobryoideae (Dicranaceae). Nova Hedwigia 45: 283–314. Williams, R. S. 1913. Dicranaceae. In: N. L. Britton et al., eds. 1905+. North American Flora.... 47+ vols. New York. Vol. 15, pp. 77–158.

1. Costa broad, occupying 1/3 or more of leaf base.
   2. Costa in cross section with a median row of chlorocysts enclosed on both surfaces by a single row of hyalocysts, this sometimes interspersed with chlorocysts on abaxial surface.
      3. Hyalocysts never interspersed with chlorocysts; plants yellowish or greenish; clusters of linear, twisted brood leaves in axils of upper leaves . . . . . 4. *Brothera*, p. 365
      3. Hyalocysts sometimes interspersed with chlorocysts on abaxial costa surface; plants often whitish green, sometimes yellowish green; clusters of brood leaves absent . . . . . 15. *Paraleucobryum*, p. 425
   2. Costa in cross section with a row of guide cells and stereid bands of cells.
      4. Costa often without stereid cells above the guide cells; leaves acute or with a hyaline awn, the apex entire to serrate . . . . . 5. *Campylopus*, p. 366
      4. Costa always with stereid cells above and below the guide cells, smooth or nearly so; leaves narrowed to a long-setaceous, often serrulate apex.
         5. Leaves not deciduous; rhizoids absent on abaxial surface of costa . . . . 3. *Campylopodiella*, p. 363
         5. Leaves often deciduous; rhizoids often on abaxial surface of costa . . . 9. *Dicranodontium*, p. 393
1. Costa narrow, occupying less than 1/3 of leaf base.
   6. Plants slender and julaceous . . . . . 1. *Aongstroemia*, p. 360
   6. Plants not julaceous, leaves usually crisped, contorted, flexuose, spreading or falcate-secund.
      7. Alar cells differentiated, inflated, hyaline or sometimes brown, often 2-stratose . . . . . 11. *Dicranum*, p. 397
      7. Alar cells not differentiated, or if so, then 1-stratose.
         8. Leaves flexuose, falcate-secund or only rarely somewhat crisped when dry.
            9. Costa in cross section with stereid bands . . . . . 8. *Dicranella*, p. 386
            9. Costa in cross section without stereid bands.
               10. Capsule erect and symmetric; seta short, 3–6 mm . . . . . 2. *Arctoa*, p. 362
               10. Capsule suberect to inclined; seta long, 7–16 mm . . . . . 12. *Kiaeria*, p. 420
         8. Leaves crisped and contorted when dry.
            11. Capsule distinctly to indistinctly ribbed when dry, often strumose.
               12. Seta cygneous; capsule not strumose . . . . . 14. *Oreas*, p. 425
               12. Seta straight; capsule with or without a struma.
                  13. Leaves with laminae 1-stratose, cells smooth; capsules erect, without struma, often contracted below mouth when dry . . . . . 16. *Rhabdoweisia*, p. 428
                  13. Leaves with distal cells of laminae often 2-stratose on margins or elsewhere, papillose or smooth; capsules inclined, often strumose, sometimes contracted below mouth when dry.
                     14. Leaf laminae often 2-stratose but only on margins, rarely elsewhere, cells smooth or papillose on adaxial and abaxial surfaces; capsule with or without struma, not contracted below mouth, striate when dry . . . . . 6. *Cynodontium*, p. 376
                     14. Leaf laminae usually 1-stratose on margins but with 2-stratose regions elsewhere, cells strongly papillose, often with forked papillae; capsule always strumose, contracted below mouth and wrinkled when dry . . . . . 7. *Dichodontium* (in part), p. 382
            11. Capsule smooth or wrinkled when dry, sometimes strumose.
               15. Leaf cells with a large papilla on both adaxial and abaxial surfaces; capsules smooth . . . . . 7. *Dichodontium* (in part), p. 382
               15. Leaf cells smooth or with longitudinal cuticular thickenings; capsules smooth or wrinkled.
                  16. Plants usually small, 1–2 cm; leaves with lanceolate base; capsule not strumose . . . . . 10. *Dicranoweisia*, p. 395
                  16. Plants large, usually 2–5 cm; leaves with ovate or obovate base, often sheathing; capsule sometimes strumose.

[17. Shifted to left margin.—Ed.]

17. Sporophytes single; capsule strumose . . . . . 13. *Oncophorus*, p. 423
17. Sporophytes clustered; capsule not strumose . . . . . 17. *Symblepharis*, p. 430

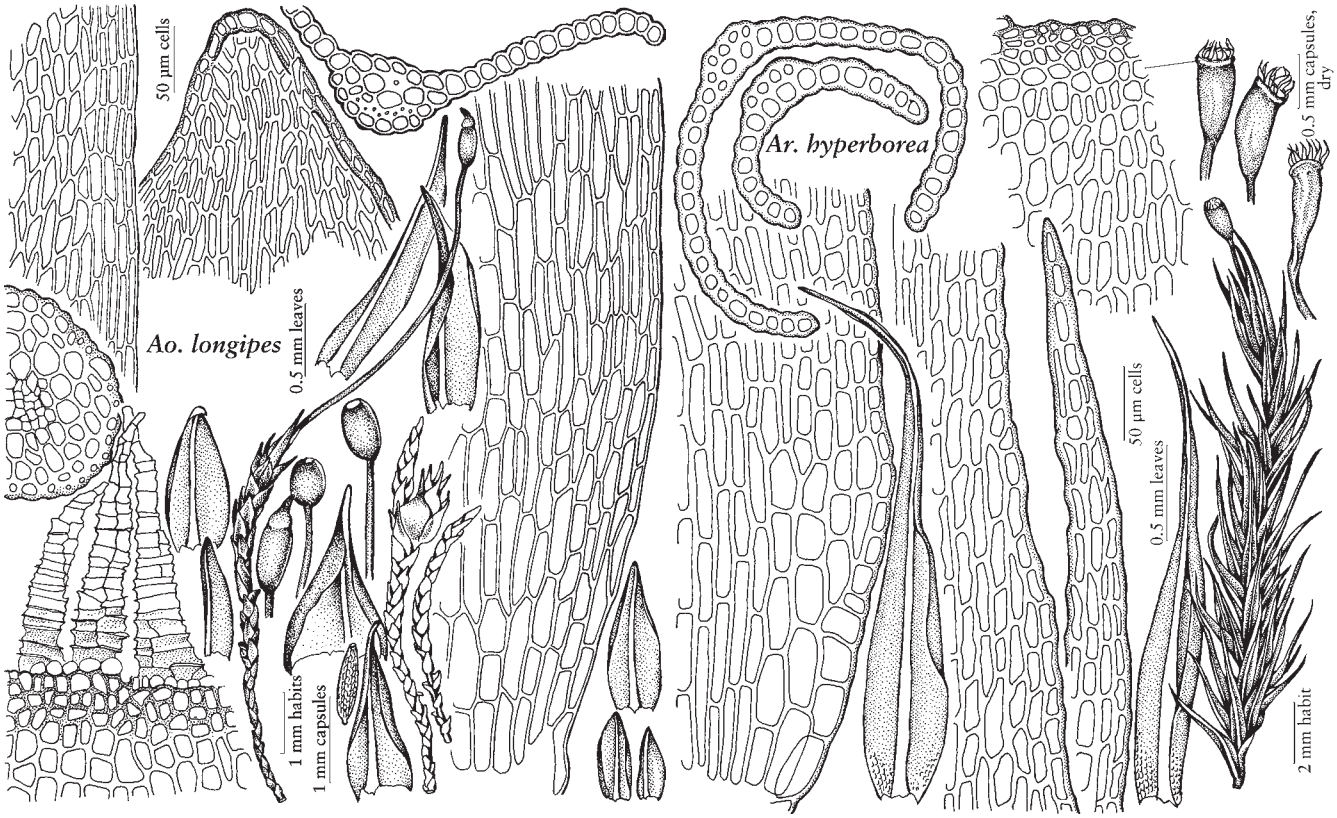
1. AONGSTROEMIA Bruch & Schimper, Bryol. Europ. 1: 171. 1846 • [For Johan Ångström, 1813–1879, Swedish bryologist]

Patricia M. Eckel

Plants small, gregarious or in loose thin mats or tufts, yellowish green, orange-red to brown-green, rather dull. **Stems** erect, 3–6(–12) mm, simple or occasionally forked, central strand present; scarcely radiculose, rhizoids red, smooth. **Leaves** ovate or shortly lanceolate-acuminate, concave proximally, tubulose when acuminate, erect and appressed-imbricate when dry, somewhat loosely so when moist; apices in proximal leaves broadly acute grading to obtuse to acuminate-subulate in distal leaves; margins plane to incurved, entire, notched at the apex; costa prominent, single, ending before the apex, smooth on all surfaces, guide cells in 1 row, stereid bands 2, the adaxial band reduced, abaxial and adaxial epidermis prominent; laminal cells convex in section, without pits, smooth, mostly elongate throughout, shorter in the apex, walls in surface view thick-walled, irregularly elongate-hexagonal, rhomboid or rectangular, alar cells undifferentiated. **Specialized asexual reproduction** absent. **Sexual condition** dioicous; perigonial plants similar to the perichaetial, perigonium terminal, conspicuous, perigonial leaves larger than the cauline leaves, broadly lanceolate-triangular with an abrupt acumination, broadly tubulose; perichaetium terminal, conspicuous, leaves larger than stem leaves, convolute-sheathing, abruptly long-acuminate to subulate. **Seta** elongate, smooth, erect, yellow-orange to red. **Capsule** erect, globose, ovate or short-cylindric, straight, symmetric, smooth wet or dry, annular cells weakly differentiated in one layer; operculum conic to short-rostrate, oblique; peristome variably absent or present, single, 16 teeth ± cleft to 1/2 the length, vertically pitted-striolate basally, weakly papillose to smooth distally, reddish brown to nearly hyaline. **Calyptra** cucullate, smooth, naked, fugacious. **Spores** 12–20 µm, smooth to finely papillose.

Species 7 (1 in the flora): North America, Mexico, Central America, South America, Eurasia, Atlantic Islands.

Aongstroemia is found in north-temperate and tropical areas. The julaceous gametophyte of *Aongstroemia* species often has been compared to similar habits of other genera, e.g., A. J. Grout's (1928–1940, vol. 1) statement, seconded by H. A. Crum (1994b), that *Aongstroemia* has the habit of an *Anomobryum* (Bryaceae) but the peristome of a *Dicranum*. The genus *Aongstroemia* highlights the rather poor differentiation of Dicranaceae from the Ditrichaceae. The latter has "peristome teeth that are divided into terete rather than flat divisions and lack vertical pit-striations" (H. A. Crum and J. A. Snider 1994). Among the genera discussed below, the only consistent distinction afforded *Aongstroemia* is the dioicous sexuality. Eperistomate species of *Aongstroemia* in Mexico, Central America, and South America may be confused with species in *Astomiopsis* Müller Hal., which also has julaceous stems, similar leaves, areolation and spores (smooth to faintly papillose) but lacks a peristome. *Astomiopsis* has autoicous rather than dioicous inflorescences, and the rather well-differentiated annulus in two rows is characteristic (J. A. Snider 1994c). Monotypic *Bryomanginia* Thériot, without a peristome, is also autoicous, with a prominent annulus, distally bistratose leaf laminae, fastigiately branched habit, and bipolar ornamented spores (proximally vermiculose, distally rugose) (J. A. Snider



AONGSTROEMIA ◦ ARCTOA

1994d). An informative discussion of these genera has been given by W. R. Buck and R. H. Zander (1980).

The highest diversity for *Aongstroemia* is in Mexico, Central America, and South America.

1. Aongstroemia longipes (Sommerfelt) Bruch & Schimper, Bryol. Europ. 1: 173. 1846 F

Weissia longipes Sommerfelt, Suppl. Fl. Lapp., 52, plate 1, figs. 1–10. 1826; *Dicranum julaceum* Hooker

Stems stiff, slenderly julaceous, sterile and young material filiform, central strand distinct. **Leaves** proximally minute, 0.5–1 mm, scalelike, becoming larger and ovate-lanceolate distally; apex obtuse, subcucullate to acuminate-subulate in distal leaves; lamina 1-stratose; costa strong, less than a quarter of the leaf width, in section hydroids absent; median laminal cells (25–)30–60 × 8–15 µm, thinner, longer and narrower at the margin and forming a smooth, non-erose, indistinct border parallel to the margin. **Perigonium** a dark knob or apical rosette wider than the stem, formed by largest leaves, incurved-tubulose, to twice the length of the cauline leaves, abruptly narrowed into a tubulose acumination that can be longer than the leaf body. **Perichaetium** a large apical tuft, the leaves larger than stem leaves, to 1.5 mm, long-lanceolate and tubulose, acuminate from a broad, sheathing base, in most distal leaves rapidly or fairly rapidly narrowed into a blunt subula. **Seta** 4–10(–12) mm. **Capsule** exserted, brown, 0.6–1 mm, without stomates; peristome entire, perforate or divided nearly 1/2 distally, more or less vertically striolate to almost smooth basally, yellow and finely papillose to smooth distally; operculum to 0.4 mm.

Capsules mature late summer. Moist, exposed, sandy or silty soil of depressions, river and stream banks in montane coniferous forest regions, subalpine regions, mountains, and northern latitudes; low to high elevations; Greenland; Alta., B.C., Nfld. and Labr. (Nfld.), N.W.T., Yukon; Alaska, Wash.; Arctic; n Europe; n Asia; Atlantic Islands (Iceland).

The only species in the genus reported for China, *Aongstroemia orientalis* Mitten of alpine regions, has been described as having an apex "sharply bent to one side at the tips" (Gao C. et al. 1999). Leaves in American populations of *Aongstroemia longipes* display this characteristic as well, although less distinctly. E. Nyholm

(1986) indicated that *A. longipes* resembles *Pohlia filum* (Schimper) Mårtensson of similar habitats in Scandinavia, but that the leaf apex is sharply pointed in *P. filum*, and obtuse in *A. longipes*. For discussion of the species' ecology see L. C. Bliss and J. E. Cantlon (1957). *Aongstroemiopsis julacea* (Dozy & Molkenboer) M. Fleischer, of Asia, differs in its autoicous sexuality, prominent excurrent costa, and lack of peristome (H. C. Gangulee 1969+, fasc. 2).

2. ARCTOA Bruch & Schimper, Bryol. Europ. 1: 151. 1846 • [Greek *arktos*, bear, alluding to an arctic or northern distribution]

Steven G. Newmaster

Dicranum sect. *Arctoa* (Bruch & Schimper) Braithwaite

Plants in dense tufts, dark green to yellowish brown, shiny. Stems (0.5–)1–2(–5) cm, branches simple, sparsely radiculose. Leaves lanceolate, subulate, erect-spreading, sometimes falcate-secund; margins erect, entire, or serrulate near the tips; costa excurrent as an awn, narrow, stereids poorly differentiated from median guide cells; distal laminal cells rectangular to subquadrate, smooth or slightly mammillose; basal laminal cells elongate, smooth, sometimes porose, alar cells sometimes differentiated and inflated. **Perichaetial leaves** with a sheathing base. **Sexual condition** autoicous. **Seta** solitary, 3–6 mm, erect, stout, yellow. **Capsule** erect, exserted or immersed in perichaetial leaves, symmetric, obovoid, constricted below mouth, furrowed when dry, urn 0.5–1.2 mm; operculum obliquely rostrate; peristome single, of 16 red-brown teeth, divided halfway into two segments, vertically or irregularly striolate. **Calyptra** cucullate, smooth. **Spores** spheric, 16–30 µm, finely roughened, green.

Species ca. 4 (3 in the flora): North America, Europe, Asia.

A rare northern and alpine genus, *Arctoa* occurs on rock or soil and is distinguished by its medium-sized, *Dicranum*-like habit, with poorly differentiated stereid and guide cells. It may be confused with *Kiaeria,* which differs by a longer seta, and capsules often strumose, with narrow mouths.

SELECTED REFERENCE Allen, B. H. 1998. The genus *Arctoa* (Musci: Dicranaceae) in Maine. Evansia 15: 131–137.

1. Peristome teeth not wide-spreading; distal leaf cells 1–2:1; costa short-excurrent . . . . . 3. *Arctoa hyperborea*
1. Peristome teeth wide-spreading; distal leaf cells 2–5:1; costa long-excurrent.
   2. Capsule straight, immersed; seta short; awn entire . . . . . 1. *Arctoa anderssonii*
   2. Capsule curved, exserted; seta long; awn toothed . . . . . 2. *Arctoa fulvella*

1. Arctoa anderssonii Wichura, Flora 42: 432, plate 7, figs. 3–8. 1859

Arctoa fulvella var. *anderssonii* (Wichura) Grout

Plants small, in compact, yellow-brown or green tufts. **Stems** (0.5–)1–2(–4) cm. **Leaves** erect spreading or falcate-secund, lanceolate, subulate, 2–3 mm; costa 30–55 µm wide at base, long-excurrent, rough near tip; distal laminal cells mostly quadrate (2–5:1), incrassate; basal laminal cells elongate, alar cells differentiated. **Perichaetial leaves** much larger than stem leaves. **Seta** short, 1–3 mm. **Capsule** immersed in perichaetial leaves, straight; peristome teeth spreading outward when dry. **Spores** 16–27 µm.

Capsules mature summer. Siliceous rock; high elevations; Greenland; Yukon; Europe.

A rare high-arctic species, *Arctoa anderssonii* was once considered a variety of *A. fulvella,* but is distinguished by a short seta, large perichaetial leaves, and straight, immersed capsule. It has a costa that is more shortly excurrent than that of *A. fulvella* but longer than that of *A. hyperborea*.

2. Arctoa fulvella (Dickson) Bruch & Schimper, Bryol. Europ. 1: 156. 1846

Bryum fulvellum Dickson, Fasc. Fl. Crypt. Brit. 4: 10, plate 11, fig. 1. 1801; *Dicranum fulvellum* Smith

Plants small, in compact, moderately shiny, yellow-brown or green tufts. **Stems** (0.5–)1–2 (–4) cm. **Leaves** erect or falcate-secund, lanceolate, subulate, 2–3 mm; costa 30–60 µm wide at base, very long-excurrent, rough near tip; distal laminal cells mostly rectangular (2–5:1), incrassate; basal laminal cells elongate, alar cells differentiated. **Seta** long, (3–)4–6(–7) mm. **Capsule** exserted, slightly curved, obscurely to distinctly ribbed when dry, annulus of 2 rows of cells; peristome red, spreading outward when dry. **Spores** 16–28 µm.

Capsules mature summer. Siliceous rock or soil; moderate to high elevations; Greenland; Alta, B.C, N.B., Nfld. and Labr. (Nfld.), N.W.T., N.S. Que, Yukon; Alaska, Idaho, Maine, Mont., N.H., N.Y., Oreg., Wash.; Europe; Asia.

Arctoa fulvella occurs frequently on mountain summits and exposed ledges, and is often found in late snowbed communities with *Kiaeria falcata*. Superficially it resembles *Blindia acuta*, which is distinguished by enlarged, orange alar cells and dark brown peristome teeth that do not flare conspicuously outward. *Dicranella heteromalla* vegetatively resembles *A. fulvella,* but its inclined capsules and boreal rather than alpine habitat will separate them. The long-excurrent costa distinguishes this species from other *Arctoa* species.

3. Arctoa hyperborea (Gunnerus ex Withering) Bruch & Schimper, Bryol. Europ. 1: 157. 1846 F

Bryum hyperboreum Gunnerus ex Withering, Syst. Arr. Brit. Pl. ed. 4, 3: 811. 1801; *Cynodontium hyperboreum* (Gunnerus ex Withering) Hagen; *Dicranum hyperboreum* (Gunnerus ex Withering) Smith

Plants in compact, dark green tufts. **Stems** 1–3(–5) cm. **Leaves** erect-spreading, lanceolate, subulate, 2–3 mm; costa 30–55 µm wide at base, short-excurrent, rough near tip; distal laminal cells mostly subquadrate (1–2:1), incrassate; basal laminal cells elongate, alar cells differentiated, quadrate or slightly enlarged. **Seta** 4–6(–8) mm. **Capsule** exserted, slightly curved, obscurely to distinctly ribbed when dry, annulus developed, separating; peristome large, not spreading outward when dry. **Spores** 18–30 µm.

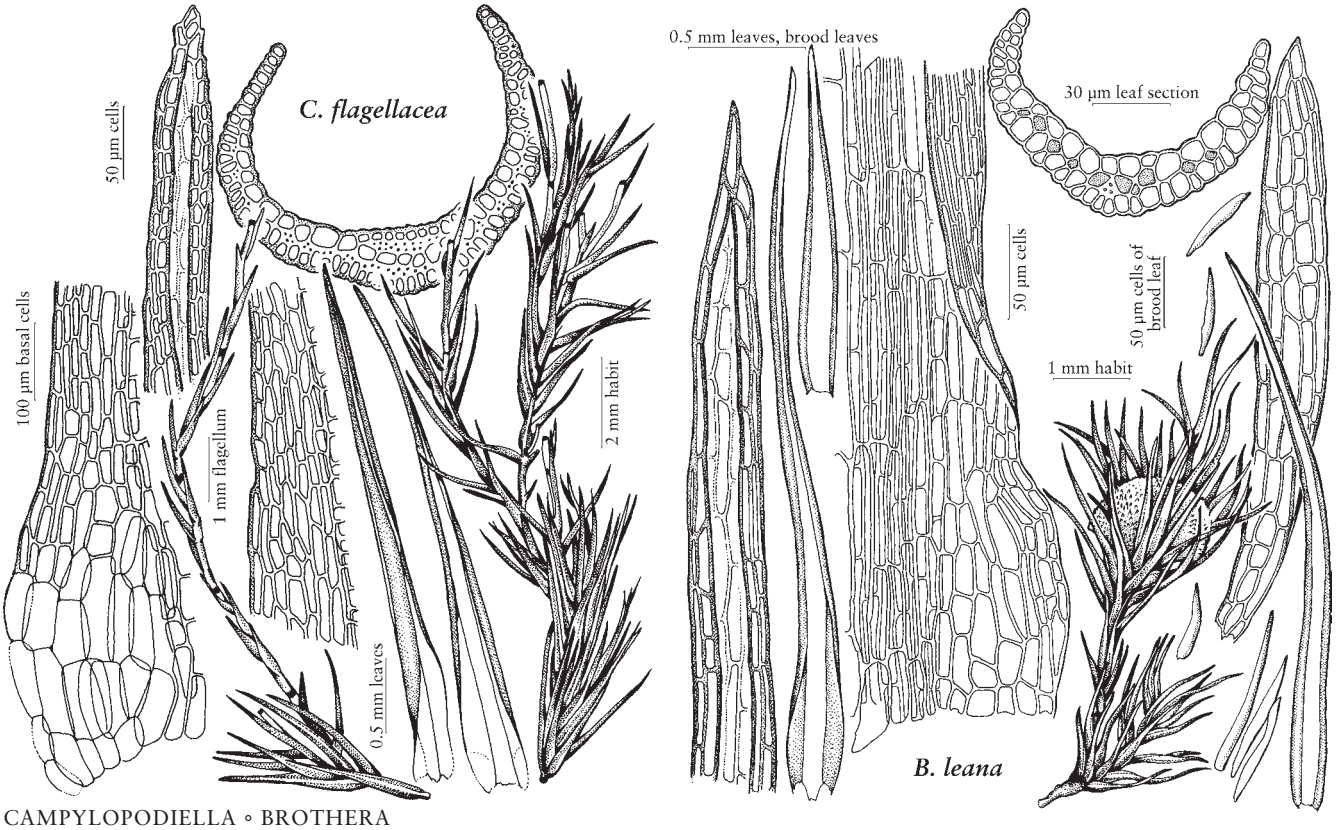
Capsules mature summer. Siliceous rock or soil; high-alpine elevations; Greenland; Europe.

Arctoa hyperborea is a rare arctic-alpine moss found on rock ledges or crevices at high elevations. It is distinguished from other species of the genus by its short-excurrent costa, shorter seta (the length is highly variable), and peristome not spreading when dry.

3. CAMPYLOPODIELLA Cardot, Bull. Herb. Boissier, sér. 2, 8: 90. 1908 • [Genus *Campylopus* and Latin *-ella*, diminutive]

Jan-Peter Frahm

Plants in loose to compact tufts, 5–30 mm. **Stems** radiculose. **Leaves** erect-patent, lanceolate, ending in a long acumen, entire or with a few teeth at tips; costa filling 1/2–2/3 of the leaf base, excurrent, in transverse section with large adaxial and abaxial hyalocysts, a median band of chlorocysts and 2–4 adaxial stereids; alar cells weakly developed; laminal cells long-rectangular. **Sexual condition** dioicous; perigonial leaves from broader base suddenly contracted into a slender subula. **Seta** yellowish or brownish in age, erect, twisted distally. **Capsule** erect, elliptic to cylindric, yellowish, without stomata; operculum long-rostrate; annulus present; peristome teeth 16, divided nearly to the base. **Calyptra** cucullate, fimbriate or entire at base. **Spores** 11–19 µm.



CAMPYLOPODIELLA ◦ BROTHERA

Species 4 (2 in the flora): North America, Mexico, Central America, South America, Asia.

The species listed here were previously included in the genus *Atractylocarpus* Mitten because of considerable confusion involved with the use of that generic name (J.-P. Frahm 2000). This was caused by the fact that the type species of *Atractylocarpus* turned out to belong to a genus later described as *Campylopodiella*. Therefore Frahm and P. Isoviita (1986) proposed conservation of the name *Atractylocarpus*, which was, however, rejected by the nomenclature committee at the International Botanical Congress in Tokyo. That decision was later corrected at the Congress in St. Louis, thus preserving the use of the name as proposed before, making new combinations unnecessary.

Campylopodiella comprises three species in the Himalayas, Central America, and northern South America, of which two have been found also in the flora area, each with one record. One species is also known from Eocene Baltic amber, which is presumably identical with the extant species from the Himalayas. The genus is characterized by a unique transverse section of the costa with a median band of chlorocysts and a few ventral stereids, which can be seen under the microscope without transverse section as dark band in the middle of the costa.

1. Alar cells distinct, inflated; leaves 5–8 times as long as wide; basal laminal cells in about 6 rows . . . . . 1. *Campylopodiella flagellacea*
1. Alar cells indistinct; leaves 10–13 times longer than wide; basal laminal cells in 15–18 rows . . . . . 2. *Campylopodiella stenocarpa*

1. Campylopodiella flagellacea (Müller Hal.) Frahm & Isoviita, Taxon 37: 968. 1988 F

Dicranum flagellaceum Müller Hal., Syn. Musc. Frond. 2: 597. 1851; *Atractylocarpus flagellaceus* (Müller Hal.) Williams

Plants erect, yellowish green, in tufts. **Stems** 3–15 mm, radiculose. **Leaves** erect-patent when wet, appressed when dry, 1.8–2.3 mm, 5–8 times as long as wide, lanceolate, gradually contracted, margins entire, only slightly denticulate at the extreme apex; costa filling 1/2–2/3 of the leaf base, 155 µm wide and indistinctly delimited at base, filling most parts of the leaf apex, excurrent, in transverse section with large adaxial and abaxial hyalocysts, a median band of stereids and 2–4 stereids adaxially; alar cells hyaline or brownish, often 2-stratose, slightly inflated; basal laminal cells in about 6 rows, rectangular, 15–40 × 10–16 µm, narrower at margins; distal laminal cells rectangular, 13–30 × 4–12 µm.

Soil, earth covered rocks, bases of trees, moderate elevations (300–500 m); Calif.; Mexico, Central America; South America (Andes).

Sporophytes of *Campylopodiella flagellacea* have been found only once, in South America. The only North American record was collected on a seeping roadside rock in Trinity County (*Shevock 17741,* BONN). That specimen differs from Central American specimens in its more compact tufts and the lack of flagelliferous branches. The species was earlier regarded as a sterile flagelliferous expression of *C. stenocarpa* by M. Padberg and J.-P. Frahm (1985), but later was treated as separate by Frahm (1991). It differs from *C. stenocarpa* in its sterile condition, shorter leaves, narrower lamina, and more distinct alar cells.

2. Campylopodiella stenocarpa (Wilson) P. Müller & J.-P. Frahm, Nova Hedwigia 45: 290. 1987

Trichostomum stenocarpum Wilson in B. Seemann, Bot. Voy. Herald, 344. 1857; *Atractylocarpus costaricensis* (Müller Hal.) R. S. Williams; *A. stenocarpus* (Wilson) Zander

Plants yellowish green, in loose tufts. **Stems** erect, 8-15 mm, radiculose proximally, erect-patent or curled when dry. **Leaves** 3.5–5 mm, 10–13 times longer than wide, narrowly lanceolate, gradually narrowed from an ovate base into a long acumen, entire at margins except for a few teeth at the extreme tip; costa filling 1/3–2/3 of the leaf base, 175–200 µm wide, excurrent; alar cells weakly differentiated; basal laminal cells in 15–18 rows, hyaline, thin-walled, rectangular, 49–95 × 4–20 µm, narrower at margins; distal laminal cells elongate, 74–140 × 4–7.5 µm. **Sexual condition** dioicous; perichaetial leaves suddenly contracted from a broadly ovate base. **Seta** erect, 8–19 mm, sinistrorsely twisted distally. **Capsule** long-cylindric, 2.5–3 × 0.4 mm, yellowish or brownish with age; exothecial cells incrassate, rectangular; operculum long-rostrate, reddish brown, 1–1.2 mm; peristome teeth 16, divided almost to the base, yellowish brown, lighter at tips, striate proximally, papillose at tips, about 290 µm. **Calyptra** cucullate, entire at base. **Spores** yellowish green, 11–13 µm.

Rotten logs, stumps, soil, bases of trees, moderate elevations (100–200 m); Mo.; Central America.

Campylopodiella stenocarpa has been found only once in the flora area, in Stoddard County, *Redfearn 27840,* (BONN).

4. BROTHERA Müller Hal., Gen. Musc. Frond., 258. 1901 • [For Viktor Ferdinand Brotherus, 1849–1929, Finnish bryologist]

Jan-Peter Frahm

Plants small, 3–6 mm, in dense, yellowish to grayish green mats. **Stems** radiculose at base. **Leaves** erect-patent when dry, lanceolate, gradually contracted to a short, canaliculate apex; costa filling 2/3 of the leaf base, not sharply delimited from the lamina, excurrent, in transverse section with lax abaxial and adaxial hyalocysts and a median band of stereids; alar cells weakly differentiated, hyaline; basal laminal cells hyaline, of 8–10 rows, 2-stratose towards the costa, rectangular; distal laminal cells rectangular. **Sexual condition** dioicous. **Seta** 5–6 mm, yellowish, sinuose and twisted sinistrorse in the distal portion. **Capsule** erect, yellowish green, 0.5 × 1.2 mm, smooth, contracted towards the peristome; annulus present; operculum rostrate, half the length of the urn; peristome teeth 16, entire or rarely perforated, yellowish, striate at base and

papillose at tips, 210–240 µm. **Calyptra** cucullate, fringed at base. **Spores** yellowish green, smooth, 10–13 µm; exothecial walls incrassate, variable, without stomata.

Species 1: e North America, Mexico, Central America, Asia, Africa.

1. Brothera leana (Sullivant) Müller Hal., Gen. Musc. Frond., 258. 1901 F

Leucophanes leanum Sullivant, Musc. Allegh., 41. 1846; *Campylopus leanus* (Sullivant) Sullivant & Lesquereux; *Leucobryum leanum* (Sullivant) Kindberg; *Syrrhopodon leanus* (Sullivant) Lesquereux & James

Leaves 2–3 mm; margins entire; costa 155–180 µm wide; basal laminal cells 19–55 × 4–19 µm, narrower at margins; distal laminal cells 24–55 × 3–7 µm. **Specialized asexual reproduction** by clusters of spindle-shaped brood leaves in the comal tufts. **Sporophytes** not found in North America.

Humic or peaty soil, rocks, especially sandstone bluffs, rotten wood, rarely bark of trees; 0–2000 m; Ark., Ill., Iowa, Ky., Md., Minn., Miss., Mo., N.C., Ohio, Pa., S.C., Tenn., Va., W.Va., Wis.; Mexico; Central America (Guatemala); Asia; Africa (Malawi).

Brothera leana is easily identified by clusters of brood leaves always present in the comal tufts. *Campylopus fragilis* has a similar appearance, but it has a different transverse section of the costa, with dorsal instead of median stereids. Furthermore, the ranges of the two species in North America do not overlap.

5. CAMPYLOPUS Bridel, Muscol. Recent., suppl. 4: 71. 1818 • [Greek *campylos*, curved, and *pous*, foot, alluding to curved seta]

Jan-Peter Frahm

Plants usually 3–10 cm, occasionally longer. **Stems** usually simple, not tomentose or with dense reddish or whitish tomentum. **Leaves** 3–12 mm, erect-patent or appressed foliate, narrowly lanceolate, ending in a smooth or denticulate, straight or reflexed tip; alar cells large, inflated, hyaline or reddish brown, or not differentiated; basal laminal cells thin-walled, hyaline, or thick-walled, chlorophyllose, sometimes with pitted walls, rectangular to subquadrate; distal laminal cell walls incrassate, quadrate to short-rectangular, oblique, or oval to elongate oval; costa strong, filling $^1/_3$–$^4/_5$ of leaf width, excurrent in a more or less long, chlorophyllose or hyaline awn, in transverse section showing a median band of deuters, an adaxial layer of hyalocysts, substereids or stereids, and abaxially layers of stereid or non-stereid cells, and an abaxial row of chlorocysts; abaxial side of the costa smooth, ridged or lamellose. **Specialized asexual reproduction** by brood leaves, microphyllous branches, deciduous leaves or stem tips or rhizoidal tubers. **Sexual condition** dioicous. **Perichaetia** terminal, often bud like, rarely pseudolateral; perichaetial leaves with a broader, sheathing base and a long, narrow subula. **Seta** 5–10 mm, those of young sporophytes curved downward, pushing the immature capsule between the comal leaves and leaving the calyptra behind when the mature capsule curves upward, sinuose, twisted, cygneous when wet and performing uncoiling movements. **Capsule** erect and symmetric or curved and asymmetric, sometimes strumose, furrowed when empty; annulus present but not dehiscent; operculum rostrate, half as long as the capsule; peristome teeth divided to the middle in two prongs, reddish or orange and horizontally striate proximally, hyaline and papillose distally. **Calyptra** cucullate, ciliate or entire at base. **Spores** ca. 13 µm, smooth or papillose.

Species ca. 180 (17 in the flora): North America, Mexico, West Indies, Central America, South America, Europe, Asia, Africa, Atlantic Islands, Pacific Islands, Australia.

The North American species of *Campylopus* were revised by J.-P. Frahm (1980) based on a study of more than 1000 herbarium specimens. At that time, four species of *Campylopus* were

recorded as new to North America and two species were placed into synonymy. The most recent checklist of the mosses of North America (L. E. Anderson et al. 1990) lists 18 species. Of these, the record of *C. zygodonticarpus* is based on a misidentification and *C. paradoxus* is a superfluous name for *C. flexuosus*, which is also included in the list. Since that time, *C. japonicus* has been newly recorded for North America, resulting in a total of 17 species, and new names have been introduced for *C. aureus*, *C. japonicus,* and *C. schwarzii*.

Campylopus was formerly divided into three subgenera on the basis of morphology of the transverse section of the costa. Although this classification is no longer used, the anatomy of the costa is still an important character for identification. It is, however, not in all cases necessary to prepare cross sections. The presence of adaxial stereids or hyalocysts can also be observed under the microscope by surface view of the adaxial side of the costa. Since the perichaetial leaves vary in both form and by the presence of thin-walled cells walls in species that usually have thick-walled cells, the study of such characters should be avoided. Alar cells are generally also not a valuable character in *Campylopus;* they are little differentiated in plants growing in damp habitats but are well developed in plants in exposed habitats with water uptake from the underground. The same is true for the presence or absence of a tomentum. Identification is facilitated if the ranges of the species are considered. Many species are found only very locally.

SELECTED REFERENCES Frahm, J.-P. 1980. Synopsis of the genus *Campylopus* in North America north of Mexico. Bryologist 83: 570–588. Frahm, J.-P. 1994. A contribution to the differentiation of *Campylopus subulatus* and *C. tallulensis* in North America. Evansia 11: 95–99. Frahm, J.-P. and D. H. Vitt. 1978. A taxonomic study of *Campylopus schimperi* and *C. subulatus* in North America. Brittonia 30: 365–372.

1. Leaf tips ending in a hyaline hairpoint.
   2. Hairpoints reflexed . . . . . 8. *Campylopus introflexus*
   2. Hairpoints straight.
      3. Basal laminal cells thick-walled, chlorophyllose, subquadrate to short-rectangular (2:1).
         4. Distal laminal cells vermicular . . . . . 3. *Campylopus atrovirens* (in part)
         4. Distal laminal cells rectangular . . . . . 14. *Campylopus sinensis*
      3. Basal laminal cells thin-walled, hyaline, long-rectangular (more than 4:1).
         5. Abaxial side of costa lamellose with lamellae 3–4 cells high . . . . . 10. *Campylopus pilifer*
         5. Abaxial side of costa smooth or ridged.
            6. Distal laminal cells oval to elongate oval . . . . . 13. *Campylopus schmidii*
            6. Distal laminal cells rectangular to obliquely rectangular.
               7. Distal laminal cells 4–6:1, plants less than 1 cm, leaves 2.5–4 mm, transverse section of costa with adaxial stereids . . . . . 4. *Campylopus carolinae*
               7. Distal laminal cells 1.5–2:1, plants to 3 cm, transverse section of costa with adaxial hyalocysts . . . . . 9. *Campylopus oerstedianus*

1. Leaf tips concolorous.
   8. Leaf tips cucullate . . . . . 3. *Campylopus atrovirens* (in part)
   8. Leaf tips plane.
      9. Basal laminal cell walls thick-walled, chlorophyllose.
         10. Basal laminal cells pitted; transverse section of costa showing adaxial stereids . . . . . 2. *Campylopus arctocarpus*
         10. Basal laminal cells with smooth walls; transverse section of costa showing adaxial hyalocysts.
            11. Distal laminal cells 6–10:1; plants distantly foliate with spreading leaves . . . . . 1. *Campylopus angustiretis*
            11. Distal laminal cells shorter; plants densely foliate with appressed leaves.
               12. Distal laminal cells short, subquadrate to rhombic; plants equally foliate . . . . . 5. *Campylopus flexuosus*
               12. Distal laminal cells short- to long-rectangular or oblique, 2–4(–6):1; plants in small rosettes or with appressed foliate leaves in a terminal comal tuft . . . . . 16. *Campylopus surinamensis*

[9. Shifted to left margin.—Ed.]

9. Basal laminal cells thin-walled, hyaline.
   13. Costa occupying 3/5–4/5 of leaf width . . . . . 7. *Campylopus gracilis*
   13. Costa 1/2 of leaf width.
      14. Distal laminal cells rectangular, ca. 4:1.
         15. Plants in small rosettes; leaves long-subulate . . . . . 11. *Campylopus pyriformis*
         15. Plants in dense cushions; leaves shortly pointed . . . . . 12. *Campylopus schimperi*
      14. Distal laminal cells shorter.
         16. Leaves widest below mid leaf; basal and distal laminal cells sharply differentiated; specialized asexual reproduction frequently by boomerang-shaped brood leaves . . . . . 6. *Campylopus fragilis*
         16. Leaves widest at leaf base; basal and distal laminal cells not sharply delimited; specialized asexual reproduction occasionally by deciduous stem tips.
            17. Costa in transverse section without abaxial stereids . . . . . 15. *Campylopus subulatus*
            17. Costa in transverse section showing distinct groups of abaxial stereids . . . . . 17. *Campylopus tallulensis*

1. Campylopus angustiretis (Austin) Lesquereux & James, Man., 80. 1884

Dicranum angustirete Austin, Bot. Gaz. 4: 150. 1879; *Campylopus delicatulus* R. S. Williams; *C. gracilicaulis* subsp. *angustiretis* (Austin) Kindberg; *C. surinamensis* var. *angustiretis* (Austin) J.-P. Frahm

Plants 5–20 mm, in loose light green to gray-green mats, evenly foliate with distant, spreading leaves, the distal ones sometimes forming a comal tuft, not tomentose. **Leaves** 6 mm, lanceolate, keeled, long-decurrent, gradually narrowed into a fine channelled, concolorous, straight tip that is denticulate at the outermost apex; alar cells large, inflated and auriculate, hyaline; basal laminal cells rectangular, moderately thick-walled, narrower and thin-walled in several marginal rows; distal laminal cells elongate, 6–10:1, not sharply delimited from the basal laminal cells; costa relatively narrow, filling 1/4–1/3 of leaf width, excurrent, in transverse section with a adaxial band of hyalocysts that are slightly smaller than the median deuters, abaxially with groups of stereids, smooth at back. **Specialized asexual reproduction** not known. **Sporophytes** not known.

Open sandy soil in wet depressions in coastal lowlands; 0–20 m; Fla.; West Indies; South America.

Campylopus angustiretis differs from all other species of the genus by its elongate distal laminal cells. Thus it is not certain if it actually belongs to this genus. Because of the lack of sporophytes a decision cannot be made. It has been treated as a variety of the sympatric *C. surinamensis* and superficially resembles certain expressions of that species (described as *C. donnellii*). It differs, however, by a narrower costa, the awn not coarsely serrate, the transverse section of the costa showing larger hyalocysts, and distinctly keeled leaves.

2. Campylopus arctocarpus (Hornschuch) Mitten, J. Linn. Soc., Bot. 12: 87. 1869

Dicranum arctocarpum Hornschuch in C. F. P. von Martius et al., Fl. Bras. 1: 12. 1840

Plants 1–3 cm, in dark green tufts, evenly foliate, stems reddish tomentose. **Leaves** 6–8 mm, erect-patent when wet, crisped when dry, lanceolate, ending in a straight concolorous tip; alar cells inflated, hyaline or (in older leaves) reddish brown; basal laminal cells rectangular, thick-walled with pitted cell walls, ca. 3–6:1, narrower and thinner walled at margins, forming a small border; distal laminal cells subquadrate to oblique or rhombic, arranged in distinct rows; costa filling up to half of the leaf width, shortly excurrent in a dentate awn, in transverse section showing abaxial and adaxial stereid bands. **Specialized asexual reproduction** by microphyllous branches. **Sporophytes** absent in flora area.

Base of trees and decaying logs, cypress swamps; ca. 5 m; Fla.; Mexico; West Indies; Central America; South America; c Africa.

Campylopus arctocarpus much resembles *C. flexuosus*, to which it seems closely related, but is distinguished mainly by the different transverse section of the costa with adaxial stereids. Other examples of the phenomenon of "sister species" differing only by the transverse section of the costa are found in the genus.

3. Campylopus atrovirens De Notaris, Syllab. Musc., 221. 1838

Plants 1–10 cm, in tall tufts, blackish proximally, yellowish brown distally. **Leaves** 4–10 mm, straight in wet and dry state, narrowly lanceolate, those of deciduous stem tips often even longer and narrower, ending in a very long subula; alar cells auriculate, hyaline or red-brown; basal laminal cells usually shortly rectangular to subquadrate, thick-walled with pitted walls, 4–8 rows of elongate hyaline cells at basal margins of leaves; distal laminal cells elongate oval to vermicular, walls incrassate; costa filling 1/2–2/3 of leaf width, excurrent in a long, straight, spinose-dentate hyaline hairpoint, in transverse section showing adaxial hyalocysts as wide as the median deuters, and abaxial groups of stereids, weakly ribbed at back. **Specialized asexual reproduction** by broken stem tips. **Seta** 4 mm. **Capsule** 1.5 mm, ovoid, brownish, operculum obliquely rostrate.

Varieties 2 (2 in the flora): North America, Europe, Asia.

Campylopus atrovirens is similar to *C. sinensis*, which differs by shorter, not vermicular distal laminal cells and shorter hyaline leaf tips. The latter has been found only once, in British Columbia, but it could be that collections of *C. sinensis* from the west coast of North America have been misidentified as *C. atrovirens*.

1. Leaves ending in a hyaline tip . . . . . 3a. *Campylopus atrovirens* var. *atrovirens*
1. Leaves ending in a cucullate apex . . . . . 3b. *Campylopus atrovirens* var. *cucullatifolius*

3a. Campylopus atrovirens De Notaris var. **atrovirens**

Leaves gradually contracted into a long, fine point, hyaline at the extreme apex.

Wet rocks, damp cliffs, seepage banks, bogs or wet humic soil, always in open habitats at sea level along the coast, or at about 1500 m in the Appalachian Mountains; 0–1500 m; B.C., Nfld. and Labr. (Nfld.); Alaska, N.C., Wash.; Europe; Asia.

The population in the Appalachian Mountains differs by greenish, not blackish plants, smaller size, less developed alar cells and less incrassate, basal laminal cell walls. Such plants have been described from similar habitats and similar elevations from the Alps of Europe as *Campylopus adustus* De Notaris. It is not known whether these populations in non-coastal areas are genotypically different or just modifications associated with higher elevations. It may perhaps deserve to be recognized at the varietal rank. Forms with falcate leaves as occurring in Europe or Asia have not yet been found in North America. Sporophytes, produced very rarely, were found in North America only once, in British Columbia

3b. Campylopus atrovirens var. **cucullatifolius** J.-P. Frahm, Bryologist 83: 574, fig. 1. 1981

Leaves with concolorous, cucullate tips.

Wet rocks; elevation not known (mountain); Alaska; Europe; Asia (China).

In North America this variety is known only from the type locality on Kuju Island, Alaska, and otherwise only from three collections from Great Britain and China. Cucullate instead of hyaline tipped leaves are found in a number of species of this genus.

4. Campylopus carolinae Grout, Moss Fl. N. Amer. 1: 249, plate 122. 1939

Plants usually less than 1 cm, in loose mats, dark green to brownish green or blackish; leaves erect-patent; stems sparsely tomentose. **Leaves** 2.5–4 mm, small, lanceolate, ending in a concolorous straight tip, convolute in the distal part, with entire margins; alar cells not or only slightly differentiated; basal laminal cells rectangular, firm-walled, hyaline, 2.5–3.5:1, indistinctly bordered at margins; distal laminal cells oblique to oval, incrassate, ca. 3–5:1; costa filling 1/3 of leaf width, excurrent in a straight, toothed, hyaline point, in transverse section showing abaxial and adaxial stereids, ridged abaxially with prominent cells. **Specialized asexual reproduction** occasionally by means of deciduous stem tips. **Sporophytes** not known in area of the flora.

Typically buried in white sand in depressions, in open pine and pine-oak forests and open grassland, coastal lowlands; low elevations; Fla., N.C.; South America (Brazil).

The disjunction for *Campylopus carolinae* of western South America–southeastern North America is also found for *C. angustiretis*, *C. surinamensis* and *C. pyriformis*, which grow in similar habitats in white sand. The type material from Brunswick, North Carolina is mixed with *C. surinamensis*, which caused confusion and recognition of this species as a variety of *C. delicatulus* R. S. Williams (= *C. angustiretis*).

5. Campylopus flexuosus (Hedwig) Bridel, Muscol. Recent., suppl. 4: 71. 1818

Dicranum flexuosum Hedwig, Sp. Musc. Frond., 145, plate 38, figs. 1–4. 1801; *Campylopus paradoxus* Wilson

Plants in dense, 1–3 cm, dark green mats, usually reddish tomentose below. **Leaves** 5–7 mm, erect-patent when wet, flexuose when dry, the distal leaves sometimes curved and secund, lanceolate, ending in a straight concolorous tip, which is serrate in the distal part; alar cells hyaline or reddish; basal laminal cells thick-walled, rectangular, ca. 4–5:1, narrower toward the margins; distal laminal cells quadrate to oblique or short rhombic; costa filling 1/2–2/3 of leaf width, in transverse section showing abaxial groups of stereids and adaxial small substereidal hyalocysts which are smaller than the median deuters. **Specialized asexual reproduction** by microphyllous branches in the axils of the distal leaves. **Sporophytes** not known in North America.

Rocks, humus covered boulders and outcrops, also humic or peaty soil; 0–1500 m; B.C.; N.C.; Central America; South America; Europe; Asia (China); c Africa.

Campylopus flexuosus has been only found in a few localities in the coastal lowlands of British Columbia and a single locality in the Appalachian Mountains. The occurrences in East Asia and British Columbia may be interpreted as relictual from the Tertiary, from which area *C. flexuosus* was—in contrast to Europe—not able to spread after the Pleistocene. The only record from the Appalachian Mountains on Flat Rock, Blue Ridge Parkway, North Carolina, is difficult to explain because many similar habitats exist near that vicinity in which the species has not been found. Before 1980, all specimens from North America, except for three labelled as *C. flexuosus,* belonged in fact to *C. tallulensis* or rarely to *C. surinamensis*. *Campylopus flexuosus*, however, differs from *C. tallulensis* by thick-walled, chlorophyllose basal laminal cells and small adaxial hyalocysts and in appearence by dark green color. *Campylopus tallulensis* has hyaline thin-walled basal laminal cells, large adaxial hyalocysts (even visible in surface view of the costa) and commonly a golden yellowish color. *Campylopus surinamensis* has longer distal laminal cells and the costa ends in a strongly dentate often subhyaline awn.

6. Campylopus fragilis (Bridel) Bruch & Schimper, Bryol. Europ. 1: 164. 1847

Dicranum fragile Bridel, J. Bot. (Schrader) 1800: 296. 1801

Plants 0.5–2 cm, yellowish green, in tufts, very densely foliate, often ending in a penicillate comal tuft, whitish tomentose. **Leaves** 4–5 mm, ovate-lanceolate, widest below the middle and contracted at base, narrowed into a more or less long straight, concolorous subula; alar cells hardly developed; basal laminal cells thin-walled and hyaline, very distinctly differentiated from the distal thick-walled and quadrate laminal cells; costa filling 1/2–2/3 of leaf width, shortly excurrent, slightly serrate at tip, in transverse section showing very wide adaxial hyalocysts (easily recognizable in surface view of the costa), filling half of the width of the costa, and abaxial substereids, slightly abaxially ridged. **Specialized asexual reproduction** by small, boomerang-shaped leaves produced in the axils of the distal leaves. **Sporophytes** not known in North America.

Rocks, humus covered boulders and outcrops, also humic or peaty soil; 0–200 m; B.C.; Ark.; Central America; South America; w Europe; Asia (China, Japan); c Africa; Atlantic Islands (Azores, Canary Islands, Madeira).

Campylopus fragilis has only been found in a few localities in British Columbia and a single locality in Arkansas. It has been reported from southeastern North America based on the presence of boomerang-shaped brood leaves at the stem tips, however, these records belong to *C. surinamensis* with similar brood leaves. *Campylopus surinamensis* differs by rectangular and nonquadrate distal laminal cells, a sharply toothed, denticulate, excurrent costa and small adaxial hyalocysts. Brood leaves are produced especially "under stress" in unfavorable conditions, especially on small, depauperate plants.

7. Campylopus gracilis (Mitten) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1870–1871: 427. 1872

Dicranum gracile Mitten, J. Linn. Soc., Bot., suppl. 1: 17. 1859; *Campylopus schwarzii* Schimper

Plants 1–8 cm, glossy yellowish green or golden green, not tomentose. **Leaves** 5–8 mm, erect when wet, appressed when dry, rarely falcate, narrowly lanceolate, ending in a long and fine, concolorous subula; alar cells conspicuous, hyaline, projecting into the costa; basal laminal cells hyaline, thin-walled, long-rectangular, lamina very short, ending at mid

leaf, distal laminal cells short-rectangular or oblique, very small; costa very broad, occupying 3/4–4/5 of leaf width, long-excurrent in a fine almost entire subula, in transverse section showing very large, lax adaxial hyalocysts filling half of the costa thickness and no abaxial stereids, faintly abaxially ridged. **Specialized asexual reproduction** by deciduous leaves or broken leaf tips. **Sporophytes** not known.

Wet soil and soil covered rocks, wet cliffs in boggy slopes in subalpine habitats; low elevations; B.C.; w Europe; e Asia.

Campylopus gracilis is easily recognized by a very broad costa, occupying 3/4 or more of the leaf width, very small shortly rectangular, distal laminal cells and large auricles projecting distinctly into the costa. In Europe, the species is found in similar situations in the highly oceanic parts as in the west coast of North America, where it is found on Queen Charlotte Islands and adjacent mainland. It is also found (as in *C. atrovirens*) in the Alps.

8. Campylopus introflexus (Hedwig) Bridel, Muscol. Recent., suppl. 4: 72. 1818

Dicranum introflexum Hedwig, Sp. Musc. Frond., 141, plate 29, figs. 1–7. 1801

Plants 0.5–5 cm, in dense mats, yellowish to olive green, tomentum present or almost absent. **Leaves** 4–6 mm, erect-patent when wet, appressed when dry, lanceolate, straight, with entire margins; alar cells absent or formed by thin-walled, hyaline to reddish, inflated cells; basal laminal cells hyaline, rectangular, thin-walled, extending higher at margins and forming a V-shaped area; distal laminal cells incrassate, shortly rectangular to oblique, chlorophyllose; costa filling 1/2–3/4 of leaf width, excurrent in a hyaline hair tip, which is conspicuously 90° reflexed, in transverse section showing adaxial hyalocysts and abaxial stereids, shortly lamellose at back with ribs 1–2 cells high. **Specialized asexual reproduction** occasionally by deciduous stem tips. **Seta** 7–12 mm, yellowish brown to brownish in age, often several sporophytes from the same plant, curved or sinuose. **Capsule** brown, 1.5 mm, slightly asymmetric and curved when empty. **Calyptra** ciliate at base. **Spores** 12–14 µm.

Soil along trails, base of trees, flat roofs of buildings, peat in bogs, sand; 0–200 m; B.C.; Calif., Oreg., Wash.; South America (Argentina, Brazil, Chile); Europe; s Africa; Pacific Islands (New Caledonia, subantarctic Islands, New Zealand); Australia.

Campylopus introflexus occurs in masses in sand dunes along the west coast of North America and throughout the Southern Hemisphere. The species was introduced in Great Britain in 1942, and since the beginning of the 1970s has been aggressively spreading through Europe. It now ranges from Iceland to Spain and from Ireland to Poland. The first record in North America dates from August, 1975, and was made on a gravel roof of a building of Humboldt University, Arcata, California. The species is undoubtedly introduced in North America and is spreading here as rapidly as in Europe. The name *C. introflexus* was used previously for *C. pilifer*, thus all old references for *C. introflexus* in North America have to be referred to that species. Also, specimens of *C. surinamensis* and *C. oerstedianus* from North America were named as *C. introflexus*. *Campylopus introflexus* is easily recognized by the reflexed hair points. Female plants have terminal perichaetial buds. Problems may rarely arise with forms from shaded habitats, in which the hairpoints are absent or so short that they are not reflexed.

9. Campylopus oerstedianus (Müller Hal.) Mitten, J. Linn. Soc., Bot. 12: 81. 1869

Dicranum oerstedianum Müller Hal., Syn. Musc. Frond. 2: 596. 1851

Plants 1–3 cm, in olive green tufts, lighter above and brownish below, evenly foliate, tomentose. **Leaves** 4–5 mm, lanceolate, gradually narrowed into a subtubulose, straight, concolorous subula; alar cells slightly differentiated, reddish or hyaline; basal laminal cells hyaline, rectangular; distal laminal cells thick-walled, subquadrate to short-rectangular or oblique; costa filling half of the leaf width, excurrent in a short, hyaline tip, which is longer in perichaetial leaves, in transverse section showing adaxial hyalocysts and abaxial stereids in groups of 2 cells, abaxially ridged. **Specialized asexual reproduction** not seen. **Sporophytes** unknown.

Soil covered rocks; ca. 50 m; N.C.; West Indies (Jamaica); Central America (Costa Rica); Europe (France, Germany, Greece, Italy).

Campylopus oerstedianus has been found only once in the flora area, in the piedmont of North Carolina. The overall distribution is very scattered and suggests a circum-Tethyan range (margins of the Caribbean and Mediterranean seas). It has been described from Europe as *C. mildei* Schimper. Plants of *C. oerstedianus* resemble *C. pilifer* in habit, with shorter hairpoints. In shady habitats the hairpoints are sometimes absent. The plants are microscopically distinguished by the slightly different shape of the distal laminal cells and the transverse section of the costa, by the lack of abaxial lamellae on the costa, smaller adaxial hyalocysts of about the diameter of the median deuter cells, and groups of abaxial stereids with only 2 instead of 4 stereid cells.

10. Campylopus pilifer Bridel, Muscol. Recent., suppl. 4: 72. 1818

Campylopus leucotrichus Sullivant & Lesquereux

Plants 0.5–3 cm long, in tufts, dirty green, olive green, or yellowish green, darker below, equally foliate, the fertile ones comose. **Leaves** 4–7 mm, erect spreading or loosely appressed, lanceolate, ending in a straight, more or less long serrate hairpoint; alar cells not differentiated or strongly developed, inflated, thin-walled, hyaline or reddish; basal laminal cells hyaline, thin-walled, rectangular, forming a V-shaped area; distal laminal cells oval to rhomboidal, ca. 2:1; costa filling 1/2–3/4 of leaf width, excurrent in a hairpoint, in transverse section showing adaxial hyalocysts and abaxial groups of stereids, abaxially with lamellae 3–4 cells high. **Specialized asexual reproduction** occasionally by deciduous stem tips. **Seta** often aggregated, about 5 mm, sinuose. **Capsule** 1.5 mm, slightly asymmetric, furrowed when dry, brownish; operculum rostrate. **Calyptra** fringed at base. **Spores** ca. 13 µm.

Acidic sandy soil and acidic rocks (sandstone, granite), rock crevices, exposed, dry habitats; 50–1500 m; Ala., Ariz., Ark., Ga., La., N.C., S.C., Tenn., Tex.; Central America; South America; s, w Europe; Asia (Sri Lanka); c Africa.

The distribution of *Campylopus pilifer* in tropical America, tropical Africa, and Sri Lanka (but not other parts of Asia) suggests a Gondwanaland origin, from where the species has extended its range into warmer parts of North America and southwestern Europe. Until 30 years ago this species was not distinguished from *C. introflexus,* and accordingly all old references from North America must be referred to *C. pilifer*. The true *C. introflexus* has been a neophyte in North America since 1975.

11. Campylopus pyriformis (Schultz) Bridel, Bryol. Univ. 1: 471. 1826

Dicranum pyriforme Schultz, Prodr. Fl. Starg. Suppl., 73. 1819

Plants 3 mm, gregarious or in loose, low tufts, forming low rosettes, appearing stemless, light to olive green. **Leaves** 3 mm, erect-patent, flexuose when dry, from lanceolate base gradually contracted into a long, fine, straight, concolorous, distinctly canaliculate subula; margins serrate in the distal part of the leaves; alar cells scarcely differentiated; basal laminal cells hyaline, thin-walled, rectangular; distal laminal cells thick-walled, rectangular, ca. 4:1; costa filling 1/2–2/3 of leaf width, excurrent, in transverse section with large, empty, adaxial hyalocysts and abaxial groups of stereids, abaxially smooth. **Specialized asexual reproduction** by colorless, multicellular, long-cylindric rhizoidal tubers, 300–700 µm long, deciduous leaves and small brood leaves produced at stem tips. **Sporophytes** not present in North America.

Bare soil, also base of trees and old pine stumps in wet acid meadows and swamp forests; 0–50 m; Fla., La., Miss.; s South America (Argentina, Brazil, Chile); w Europe; Asia (China); c, s Africa, Atlantic Islands (Azores, s Iceland, Madiera); Pacific Islands (New Caledonia, New Zealand); Australia.

The description above refers to North American plants of *Campylopus pyriformis*—specimens from other parts of its range have a somewhat different appearance. This species was first recorded for North America (T. Arts and J.-P. Frahm 1990) based on collections made by W. D. Reese. The occurrence in North America at only three localities in Louisiana and Mississippi, and an additional unpublished record from Florida, can perhaps be explained by introduction facilitated by the presence of rhizoidal tubers. It may therefore be doubted whether this species is native in North America. However, the small form found in the United States resembles a form occurring in Brazil in similar habitats, from which area it may have been introduced by birds. Similar disjunctions between Brazil and southeast North America are also found in *C. surinamensis*, *C. carolinae* and *C. angustiretis*, which all conspicuously grow together on bare, acid, white sand. *Campylopus pyriformis* was also found mixed with *C. surinamensis*, but can be distinguished by the more elongate, narrowly lanceolate leaves with a channelled apex, a long-excurrent nerve and a lamina ending at mid leaf and colorless rhizoidal tubers instead of the reddish or reddish brown ones as in *C. surinamensis*.

12. Campylopus schimperi Milde, Bot. Zeitung (Berlin) 22: 13. 1864 F

Campylopus subulatus var. *schimperi* (Milde) Husnot

Plants 1–3 cm, in compact tufts, light green above, brownish and tomentose below. **Leaves** 2.5–5 mm, appressed, from a narrow base gradually contracted to an acute, straight, concolorous subula; alar cells little differentiated, only slightly wider than the basal laminal cells; basal laminal cells thin-walled, hyaline, rectangular, at margins narrower, forming a small band; distal laminal cells chlorophyllose, rectangular, ca. 4:1; costa filling 1/2–2/3 of leaf width, shortly excurrent, in transverse section