

3a. *Trichostomum tenuirostre* (Hooker & Taylor)
Lindberg var. *tenuirostre*



Barbula wollei Austin; *Didymodon wollei* (Austin) Austin; *Oxystegus cylindricus* (Bridel) Hilpert; *Trichostomum cylindricum* (Bridel) Müller Hal.

Gemmae absent.

Capsules mature fall. Soil, sandstone, calcareous rock, bluffs, boulders, under overhanging ledges, seepage areas, logs; low to high elevations (0–2300 m); B.C., N.B., N.W.T., Ont.; Ala., Alaska, Ariz., Ark., Calif., Colo., Iowa, Ky., Maine, Md., Mass., Mich., Mo., Mont., N.H., N.Y., N.C., Ohio, Pa., Tenn., Tex., Vt., Va., Wash., W.Va.; Mexico; West Indies; Central America; South America; Arctic; Eurasia; Africa; Indian Ocean Islands; Pacific Islands (Hawaii, New Zealand); Australia.

H. A. Crum and L. E. Anderson (1958) detailed the abundant variation between specimens with very narrow, often fragile (W. C. Steere 1978) leaves and those with comparatively broad leaves, the latter commonly identified in herbaria as var. *holtii* (Braithwaite) Dixon. Variety *tenuirostre* often has a thin line of hyaline cells running up each leaf margin from the differentiated proximal cells, but this is largely of a single row of cells rather than a distinctly tapering broad wing of a V. Although the Mexican type of *Trichostomum mollissimum* (Brotherus) H. A. Crum is *Pseudosymblepharis schimperiana* (Paris) H. A. Crum with typical bushy, crowded linear-lanceolate leaves, specimens from the range of the flora previously identified under the former name are *T. tenuirostre*. *Trichostomum tenuirostre*, *T. spirale*, and *T. recurvifolium* share a similar areolation by the leaves with a band of rather thick-walled rectangular cells between the thinner walled basal cells and the distal medial cells.

3b. *Trichostomum tenuirostre* var. *gemmiparum*

(Schimper) R. H. Zander, Bull. Buffalo Soc. Nat. Sci. 32: 92. 1993



Didymodon cylindricus var. *gemmiparus* Schimper, Syn. Musc. Eur. ed. 2, 165. 1876

Irregular, multicellular brown or red-brown gemmae present on adaxial surface of the leaf costa or in soil, borne on rhizoids.

Vertical dolomite; Mo.; Mexico; West Indies (Cuba, Haiti);

South America (Brazil); Europe; Asia (India).

The propaguliferous var. *gemmiparum* (R. H. Zander 1978b) has been found recently in Douglas County, Missouri (P. M. Eckel 2000) and should be looked for

elsewhere in the flora area. In Mexico, it is known from eight states (R. H. Zander 1994e).

4. *Trichostomum spirale* Grout, Moss Fl. N. Amer. 1: 162, plate 84, fig. B. 1938



Oxystegus spiralis (Grout) H. A. Crum & L. E. Anderson; *O. tenuirostris* var. *stenocarpus* (Thériot) R. H. Zander

Stem rounded-pentagonal in section. **Leaves** flattened, short-lanceolate to lanceolate, distal margins plane, entire, not bordered; apex acute, plane or

keeled; basal cells differentiated across leaf base as a U or V, commonly running up margins, not distinctly enlarged submarginally; distal laminal cells pluripapillose with low papillae; mucro conic, of 3–6 cells. **Sexual condition** autoicous. **Peristome** bluntly lanceolate.

Capsules mature fall. Rotten wood; Ont.; Mich., Minn., Wis.; Mexico; Asia.

R. H. Zander (1982, 1994d) treated *Trichostomum spirale* as a variety of *T. tenuirostre* (as *Oxystegus tenuirostris*), but the autoicous inflorescence seems significant in that differences in sexuality at the level of dioicy and monoicy are commonly found at the species level in Pottiaceae; also, the plants are slightly smaller in size and the distal medial laminal cells seem smaller (8–10 µm wide). H. A. Crum and L. E. Anderson (1980–1983) provided a summary of the problems associated with *T. spirale*; they noted that the spiral ornamentation of the peristome of this taxon is usually basal on the peristome teeth which may be papillose distally (as in *T. tenuirostre*) or completely smooth, while Zander (1982) found that peristomes of the types of *T. spirale* and its Mexican synonym *Weisiopsis stenocarpum* Thériot are within the range of variation of *T. tenuirostre*, which has variably smooth, low-spiculose, or spirally spiculose or ridged peristome teeth.

5. *Trichostomum recurvifolium* (Taylor) R. H. Zander, Bull. Buffalo Soc. Nat. Sci. 32: 92. 1993



Bryum recurvifolium Taylor, Ann. Mag. Nat. Hist. 11: 208. 1843; *Bryoerythrophyllum recurvifolium* (Taylor) R. H. Zander; *Leptodontium recurvifolium* (Taylor) Lindberg; *Oxystegus recurvifolius* (Taylor) R. H. Zander; *Paraleptodontium recurvifolium* (Taylor) D. G. Long

Stem rounded-pentagonal in section. **Leaves** flattened, long-ligulate or narrowly spatulate, distal margins plane, entire, bordered by 1–2 rows of smooth, more thick-

walled cells; apex broadly acute to rounded, plane or concave; basal cells differentiated across leaf base as a U or V, not clearly running up margins, not distinctly enlarged submarginally; distal laminal cells pluripapillose with low papillae; mucro conic, of 3–4 cells.

Not fruiting in range of the flora. Wet, organic soil; B.C.; Alaska; Europe (w United Kingdom, Ireland).

Trichostomum recurvifolium, as may be seen in the multi-genus synonymy, is clearly difficult to place with confidence. A suite of gametophyte characters and color reactions to certain chemicals, however, indicate that it is near *T. tenuirostre* (R. H. Zander 1982b). It has many of the character states of broad- and notched-leaved forms of *T. tenuirostre* sometimes segregated as var. *holtii* (Braithwaite) Dixon, including yellow-green leaves, no stem central strand (variable in *T. tenuirostre* var. *tenuirostre*), presence of a hyalodermis, leaves oblong-ligulate, leaf apex reflexed, distal margins dentate, and distal marginal cells forming a border of thick-walled cells. *Trichostomum recurvifolium*, however, differs in the somewhat longer leaf base, sharp distal marginal teeth, which have conic lumens instead of elliptic, distal laminal cells rather thick-walled, and the cells of the distal marginal row are evenly distributed and quadrate to rhomboidal, not crowded and elliptic. The northwestern Europe to northwestern North America disjunctive distribution of *T. recurvifolium* is characteristic of a group of species apparently restricted to hyperoceanic climates. This species is found on Adak Island in the Aleutian Islands.

6. *Trichostomum arcticum* Kaalaas, Bot. Not. 1900: 257. 1900



Didymodon arcticus (Kaalaas) Brotherus; *Trichostomum cuspidatissimum* Cardot & Thériot

Stem triangular in section. **Leaves** flattened, narrowly lanceolate, distal margins plane, minutely crenulate, not bordered; apex narrowly acute, plane or keeled; basal cells differentiated across leaf

base as a W, commonly running up margins, distinctly enlarged submarginally just proximal to the lowest point the quadrate medial cells extend in the leaf; distal laminal cells pluripapillose with low papillae; mucro narrowly conic, of 6–9 cells. Not fruiting in the flora area.

Gravel, fen, mire, calcareous bog, sedge meadow, low-center polygon, tundra, wet or occasionally dry areas;

often associated with snow melt runnels; moderate elevations (400–700 m); Greenland; B.C., Nfld. and Labr. (Labr.), N.W.T., Nunavut, Ont., Que., Yukon; Alaska; n Eurasia.

The triangular stem cross section with a strong central strand will easily distinguish *Trichostomum arcticum* from the disconcertingly similar *Tortella tortuosa* var. *arctica*. Additionally, the former has leaves usually strongly recurved when wet and the basal cells extend upwards both juxtacostally and marginally, while the latter has leaves weakly recurved when wet and basal cells extending upwards only towards the leaf margins. *Trichostomum arcticum* also has a distinctive area of enlarged basal cells submarginally just below the lowest point to which the quadrate distal cells extend in the leaf, and its laminal papillae are more coarse. Most species of the genus have leaf margins to some extent minutely crenulate by projecting laminal cells and their papillae, but this feature seems distinctively pronounced in *T. arcticum*, which is found generally worldwide across the arctic.

7. *Trichostomum portoricense* H. A. Crum & Steere, Bryologist 59: 250. 1956 [E]



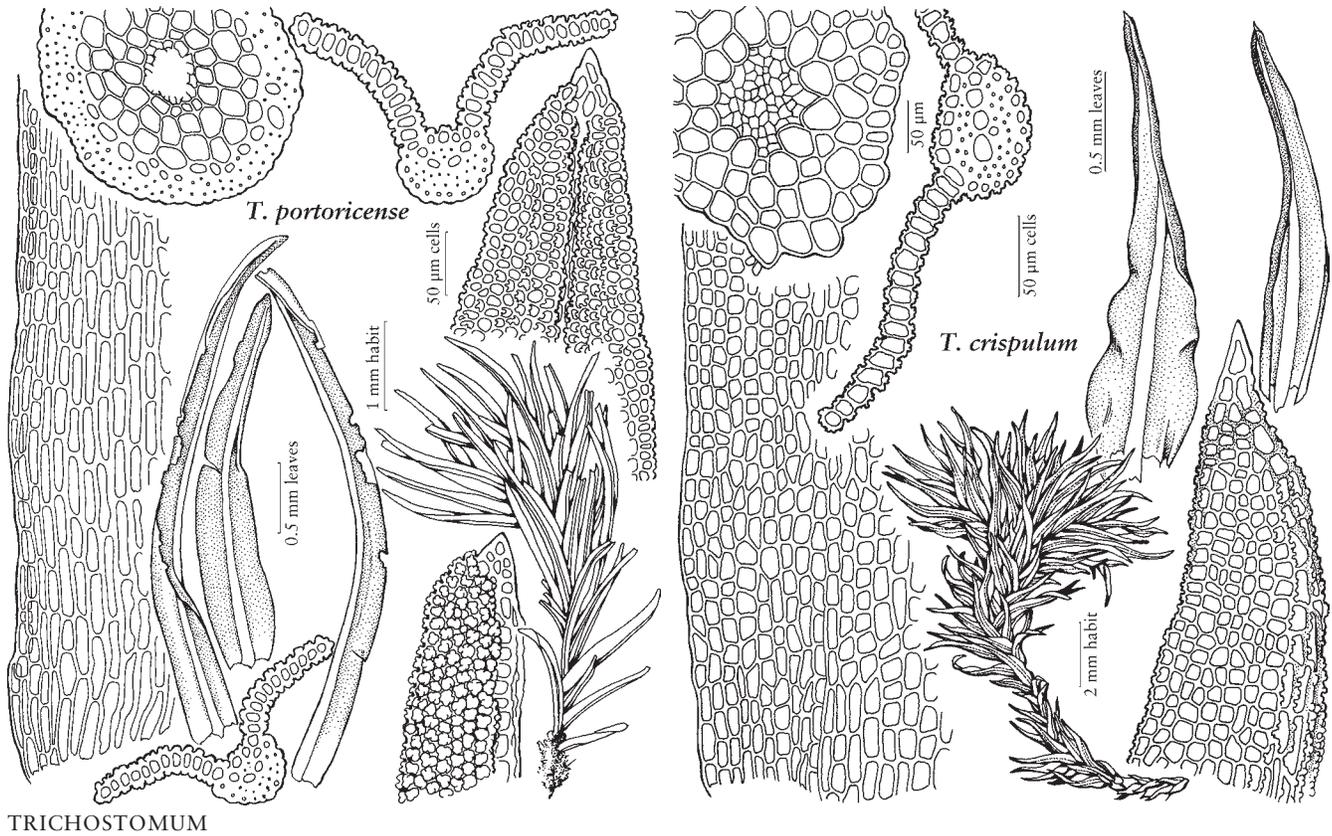
Trichostomum molariforme R. H. Zander

Stem rounded-pentagonal in section. **Leaves** flat but narrowly keeled along costa, long-ligulate, distal margins plane, entire (or tattered by fragmentation), not bordered; apex narrowly rounded, blunt, keeled; basal cells dif-

ferentiated across leaf base, not running up margins, not distinctly enlarged submarginally; distal laminal cells with a massive multiplex papillae over each lumen; mucro short-conic, of ca. 3 cells. Sterile in range of the flora.

Soil, rock, calcareous substrates; La., Tex.; Mexico; West Indies; Central America (Belize, Guatemala, Honduras).

Trichostomum portoricense is a distinctive species with no immediate relatives in the genus. The deep, narrow groove down the adaxial surface of the leaf is reminiscent of that of species of *Barbula* or *Anoetangium*. The massive, caplike papillae are similar to those of *Tuerckheimia*, but the long-ligulate leaf shape of *T. portoricense* is diagnostic. The leaf lamina fragments easily in patches, and doubtless figures in asexual reproduction. The distribution was recently summarized by P. M. Eckel (2003).



8. *Trichostomum crispulum* Bruch, Flora 12: 395, fig.

4. 1829 [F]



Stem rounded-pentagonal in section. Leaves naviculate, ovate to ovate-lanceolate or long-lanceolate, distal margins erect, entire, not bordered; apex blunt or rounded acute, seldom acute, cucullate; basal cells differentiated across leaf base as a U, commonly running up margins as a very

narrow band of nonpapillose cells, not distinctly enlarged submarginally; distal laminal cells pluripapillose with low papillae; mucro conic, of 3–6 cells. Sexual condition dioicous; known only from perichaetiate plants in the flora area.

Igneous and basic rock, soil, silt, frost boil, tundra, cliffs; Greenland; Man., N.W.T., Ont., Yukon; Ala., Alaska, Ariz., Calif., Fla., Tex., Vt.; Mexico; West Indies; Central America; Eurasia; Africa; Atlantic Islands; Pacific Islands.

Small plants of *Trichostomum crispulum* lacking sex organs may easily be mistaken for *Weissia*, but the cucullate apex and often chestnut brown costa of the former are fairly good characters. However, *Weissia crispula* Hedwig is not synonymous with *Trichostomum crispulum*. All Arctic specimens seen that had been

identified as *Weissia controversa* are referred here to *T. crispulum*. This taxon has previously been considered rare in the New World; however, it is common in Mexico (R. H. Zander 1994e), where it has been known under various synonyms. *Trichostomum crispulum* is matched in size by the similar *Weissia sharpii*, which is distinguished by the incurved distal laminal margins. *Trichostomum crispulum* in the flora area differs from populations in Europe by the stem either black or brown (in Europe usually black), the adaxial costal cells more often entirely elongate or of quadrate cells in a patch at mid leaf and the distal abaxial surface of the costa sometimes rather papillose. In Mexico, this species fruits and produces a somewhat more robust peristome than in Europe, attaining 400 to 500 µm, seldom reduced or rudimentary as it commonly is in Europe. The length of peristomes, 350–450 µm, of Japanese specimens (K. Saito 1975), however, are easily within the range of variation of American populations. *Weissia jamaicensis* has much the same well-developed peristome as does New World *T. crispulum*, and, in Mexico and portions of the southern United States, *W. jamaicensis* intergrades with *T. crispulum*, having broadly lanceolate leaves with weakly inflexed distal margins, though retaining the characteristic strong and bulging adaxial stereid band of the costa. The merely erect (not sharply incurved) leaf margin of *T. crispulum* reveals the characteristic nonpapillose margin

about 1 cell wide extending from the base to mid leaf. This also occurs in *T. brittonianum*. The specimens identified as *T. brittonianum* from Florida are, however, sterile and are not gametophytically distinct from *T. crispulum*.

Excluded Species:

Trichostomum brittonianum R. H. Zander, Bull. Buffalo Soc. Nat. Sci. 32: 92. 1993 [new name for *Hymenostomum flavescens* E. Britton in N. L. Britton and C. F. Millspaugh, Bahama Fl., 485. 1920; *Weissia flavescens* (E. Britton) W. D. Reese]

The report of this species from the flora area (Key West) by W. D. Reese (1991) remains doubtful. The sterile Key West specimens agree with the Bahamian type in the several-celled apiculus, and the clear, nonpapillose quadrate to short-rectangular cells running up the proximal leaf margins in 1–3 rows. Gametophytically, the eperistomate *T. brittonianum* is indistinguishable from the peristomate *T. crispulum*, so presence of the former in the flora area is not yet established.

Trichostomum subdenticulatum Austin, Bot. Gaz. 3: 29. 1878, not Müller Hal. 1851

The type of this forgotten name could not be found by curators of BM, BUF, FH, MANCH, and MO.

5. TUERCKHEIMIA Brotherus, Öfvers. Finska Vetenskaps-Soc. Förh. 52A(7): 1. 1910

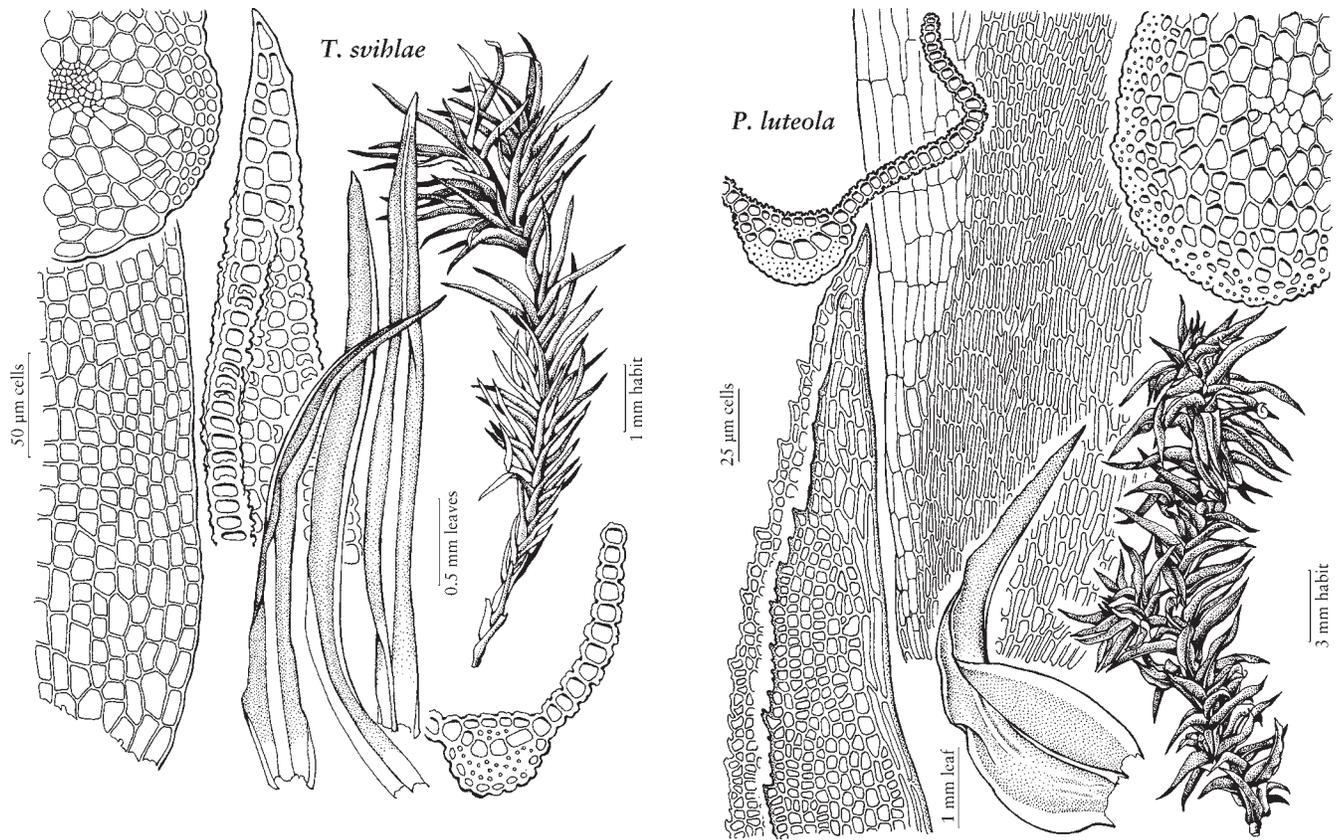
- [For Hans von Türckheim, 1853–1920, plant collector in Guatemala and West Indies]

Patricia M. Eckel

Plants in turfs, light to dark green with a somewhat bluish cast, glaucous. **Stem** to 2.5 cm, hyalodermis rarely distinct, sclerodermis absent or weakly developed, central strand present; axillary hairs to 16 cells long, basal cell occasionally brown, other axillary hair cells hyaline. **Leaves** crowded in the stem apex, spreading from the base with incurved tips, weakly contorted to crisped when dry, widespreading when moist; oblong to linear-lanceolate, with lamina often of even width to the base, subtubulose, to 3.2 mm; base undifferentiated to short-ovate; margins plane to weakly incurved, entire or occasionally deeply lobed-dentate, sometimes with 2-stratose areas; apex acute, often narrowly so; costa percurrent and ending in an apiculus or excurrent as a stout, short to elongate mucro, adaxial outgrowths absent, adaxial superficial cells quadrate to short-rectangular, 4–6 cells across costa at mid leaf; transverse section circular to ovate, adaxial epidermis present, adaxial stereid band distinct, 2 or more guide cells in one layer, hydroid strand absent, abaxial stereid band distinct, semicircular to lunate, abaxial epidermis occasionally present, weak; proximal laminal cells weakly differentiated in a small group, rectangular, somewhat larger than distal cells, 1–2:1, walls evenly thickened; distal laminal cells subquadrate, hexagonal to elliptical, ca. 10–14 µm wide, 1:1(–2); papillae typically massive, variously lobed or simple to multifid; cell walls evenly thickened, lumens rounded to subangular, superficial walls subconvex. **Specialized asexual reproduction** absent. **Sexual condition** dioicous. **Perichaetia** terminal, leaves abruptly sheathing at the base, otherwise similar to cauline leaves. **Seta** to 8 mm. **Capsule** stegocarpous, theca ellipsoidal to short-cylindric, ca. 1–1.5 mm, annulus of persistent non- or strongly vesiculose cells; operculum long-rostrate of cells in straight rows; peristome absent or rudimentary, papillose. **Calyptra** unknown. **Spores** 8–13 µm. **Laminal KOH color reaction** yellow.

Species 4 (1 in the flora): se United States, Mexico, Central America, e Asia.

Tuerckheimia was considerably revised by R. H. Zander (1978). It is characterized by narrow leaves with acute apices, plane margins and peculiar, massive papillae, best seen in the distal portion of the leaf. *Tuerckheimia calculosa* R. H. Zander & P. M. Eckel of the West Indies and Mexico, which possesses similar papillae characteristics, has been transferred to its own monotypic genus [*Quaesticula navicularis* (Mitten) R. H. Zander] on the basis of ligulate leaves with cucullate apices and strongly involute margins, subpercurrent costa, and well-developed peristome (Zander 1993).



TUERCKHEIMIA • PLEUROCHAETE

1. *Tuerckheimia svihlae* (E. B. Bartram) R. H. Zander,
Bull. Buffalo Soc. Nat. Sci. 32: 94. 1993 [F]



Trichostomum svihlae E. B. Bartram,
Rev. Bryol. Lichénol., n. s. 23: 245.
1954; *Oxystegus svihlae* (E. B.
Bartram) H. C. Gangulee;
Tuerckheimia angustifolia (K. Saito)
R. H. Zander

Plants dull blue-green above, pale tan below, often pale yellow-green or in some environments all yellow, frequently finely white-powdered with calcareous deposit. **Stems** 0.5–1(–2) cm, irregularly branched, central strand weak; tomentose. **Leaves** linear-lanceolate, occasionally strap-shaped, 2–2.7(–4) mm; proximal region not differentiated or short-ovate, margins plane, entire, sinuate or shallowly sinuate-notched, apex long and narrowly acuminate, weakly channeled; costa short to long excurrent as a stout, sharp, conical mucro or subula, rarely subpercurrent; proximal laminal cells 12–17 µm wide, 2–3:1; distal laminal cells irregularly rounded-quadrate to angular-hexagonal, often horizontally elongate, (7–)10–12 µm wide, 1:1(–2), evenly thick-walled, superficial walls with thickenings forming

high knobs or pads, marginal laminal cells not differentiated from medial cells or somewhat smaller, smooth or low-papillose, papillae when present massive, compounded of blunt lobes, centered over the cell, 1–2(–3) per lumen. **Sporophytes** not known from North America.

Moist, calcareous rocks, dolomitic and limestone bluffs, limestone coves and sinks, caves, stream margins in hard and softwood forests; low to moderate elevations (50–1000 m); Ark., Fla., Ky., N.C., Tenn.; Mexico (Jalisco, Nuevo León, Tamaulipas); Asia (China, Japan, Korea).

The leaf cells of *Tuerckheimia svihlae* having massive, centered, pillow-like papillae distinguish most specimens from similar taxa, which generally have lumens obscured by various densities of small, simple to 2-fid papillae. The frequently elongate, rounded fingerlike apical mucro on the leaf (up to and exceeding 26 µm in length) is distinctive. The specimen from Alaska cited by R. H. Zander (1978c) and mentioned later (Zander 1994f) was redetermined to be *Didymodon vinealis* (Zander, pers. comm.). *Tuerckheimia svihlae* is most often confused with *Molendoa sendtneriana* (Z. Iwatsuki and A. J. Sharp 1958; K. Saito 1972b), which has dense, small and simple papillae, a costa that is seldom excurrent, an apex that is

generally flat and apiculate. The costa of *Tuerckheimia sviblae* is regularly excurrent into a stout, conic mucro and the apex is channeled by erect or up-turned margins. The tufts of *T. sviblae* are yellower than the blue-green of the *Molendoa* species; those of *T. sviblae* are less coherent and often disintegrated, the stem leaves appearing flaccid and more chaotically twisted when dry. Specimens of *Gymnostomum* and *Hymenostylium* often have only subpercurrent to short-excurrent costae, as well as scattered simple to 2-fid papillae. *Hymenostylium recurvirostrum* is similar in the irregularly angular, pellucid laminal cells but is also distinguished by the absence of an adaxial costal epidermis, the absence of a stem central strand, and presence of red tomentum on the stem. Occasionally the papillae of *Tuerckheimia sviblae* are reduced to a smooth lens-shaped cap on the lumen surface. Another distinctive character is the leaf

base commonly not distinguished in shape or areolation. When some differentiation is evident, it is in the basal $\frac{1}{8}$ – $\frac{1}{6}$ of the leaf, whereas in other species it extends much higher—to $\frac{1}{4}$ the leaf length. *Trichostomum tenuirostre*, which may have similar long, ribbonlike leaves, has a distinctive *Tortella*-like leaf like leaf base of lax, hyaline cells usually extending somewhat up the margins and scattered small laminal papillae. *Amphidium mougeotii* and *A. lapponicum* are similar to *Tuerckheimia sviblae* in leaf length and shape. *Amphidium mougeotii* has papillae over the basal cells arranged in striations, while *A. lapponicum* has dense, small, sharp papillae over the laminal leaf surface and not concentrated over the cell lumen; the stems of both are red-tomentose, have relatively dark, clear green leaves, and the proximal cells of the leaves are more strongly differentiated from the medial distal cells.

6. PLEUROCHAETE Lindberg, Öfvers. Kongl. Vetensk.-Akad. Förh. 21: 253. 1864

- [Greek *pleura*, side or rib, and *chaite*, long hair or mane, alluding to laterally borne sporophytes]

Patricia M. Eckel

Barbula sect. *Pleurochaete* (Lindberg) Müller Hal.

Plants coarse, robust, forming deep, loose turfs, distally sordid yellow-green, proximally pale to dark brown. **Stems** 3–4(–6) cm, ascending from a prostrate base, sparsely and irregularly branched, hyalodermis present, inconspicuous, sclerodermis of 2–4 rows of thickened cells, central strand with a few, small, thin-walled cells, axillary hairs all hyaline, to 15 cells in length, tomentum lacking. **Leaves** strongly and loosely incurved-contorted when dry, squarrose-recurred beyond the erect, sheathing base when wet; narrowly to broadly oblong-lanceolate, distally broadly channeled to tubulose, base erect, broadly oblong-ovate, gradually tapering to the narrow 1–2-twisted limb; margins undulate, incurved to plane, in the distal region regularly to irregularly denticulate-serrulate, lamina 1-stratose throughout, bordered in the proximal $\frac{1}{4}$ – $\frac{3}{4}$ region with elongate, hyaline, thin-walled rhomboidal cells in a band 4–10 cells wide, widest in the basal region at the abaxial angle of base and limb, strongly narrowed proximally to the leaf insertion with cells becoming quadrate to short-rectangular, marginal band narrowing distally and disappearing into the limb, the border smooth throughout or distally the cells becoming irregularly serrulate at their distal ends, the serrulations extending into the distal region of chlorophyllose cells; apex gradually acuminate and short-aristate with smooth margins to broadly acute and mucronate; costa excurrent as a short, pointed awn or mucro, covered adaxially with quadrate, papillose cells, abaxially elongate and smooth; transverse section semicircular to reniform, adaxial epidermis present, adaxial stereid band present, robust, guide cells 4–6 in 1 layer, hydroid strand absent, basal cells (4)–6–7(–10):1, echlorophyllose and hyaline, walls as

thick as distal cells, smooth, often porose juxtacostally, distal cells subquadrate, 7–12(–14) μm wide, chlorophyllose, evenly thickened, densely papillose, papillae dense, 2-fid, 1–4 per lumen, cells of basal margin forming a border of oblong or oblong-linear, large, inflated, thin-walled and hyaline cells. **Specialized asexual reproduction** none. **Sexual condition** dioicous; perichaetia and perigonia lateral, at the apex of small branches; perichaetial leaves similar to the cauline, somewhat narrower. [Seta to 1.7 cm. **Capsule** stegocarpous, theca erect, cylindrical; annulus persistent; operculum bluntly high-conic or conic-rostrate; peristome divided to the base into 32 brownish orange, branched-spiculose, filiform divisions, loosely twisted counterclockwise in 1 turn. **Calyptra** cucullate. **Spores** spherical, moderately papillose, 10–13 μm .] **KOH reaction** pale lemon-yellow.

Species 2 (1 in the flora): temperate North America, Mexico, West Indies, Central America, South America, Europe, n, c Africa, Atlantic Islands (Azores, Canary Islands), Asia (including the Middle East).

A review of specimens of this genus worldwide, including the type specimens and protologues of *Pleurochaete malacophylla* (Müller Hal.) Brotherus and *P. ecuadorensis* Brotherus, and numerous specimens of *P. beccarii* Venturi, indicates that the genus comprises a species complex, *P. squarrosa* (Bridel) Lindberg in the loose sense. However, in the New World there is a facies, *P. luteola*, that is variable around a norm displaying a hyaline marginal band reaching farther in the proximal part of the leaf (usually reaching $1/2$ – $2/3$ leaf length), with corresponding stronger serrations in the distal part of the band. No other difference, including the habit of the leaves on the stem in the dry state or size of stem central strand, could be identified apart from basal cell length being more extreme in well-developed *P. luteola*. Variation fluctuates above and below the average of $1/2$ of the leaf length for marginal band length. In the Old World, these characters are reduced: the norm is a shorter marginal band relative to the leaf length, just short of $1/2$ the leaf length in its best expression (it is usually $1/8$ to $1/6$). There is generally little or usually no dentition at the distal terminus of the hyaline band. Small or depauperate plants display extreme reduction as they do in the New World, but in *P. squarrosa* the hyaline band is nearly absent. R. H. Zander (1993) treated *P. luteola* as a variety of *P. squarrosa*, but due to the size of geographic distribution separating these two facies, *P. luteola* is here retained at the species level and *P. squarrosa* is excluded from the New World. Specimens from North and South America with relatively shorter marginal bands, broader and shorter leaves and other variation may be interpreted as simply the low end of New World variation of *P. luteola*. Even in plants with small leaves, the marginal band extends higher up the leaf, at least in some leaves, in specimens from the New World than specimens with small leaves from the Old World. There are no robust specimens of *P. squarrosa* in the strict sense in the New World.

The genus is distinct from *Tortella*, which it closely resembles, by the hyaline basal cells not in a true V-shape, but present only on the basal margins as two clear membranaceous linear strips different from the colored, thick-walled basal cells interior to them, also by the absence of radicles cloaking the stem, the denticulate-serrulate distal leaf margins, and the axillary inflorescences. The genus resembles the Pottiaceous genera *Molendoa* and *Anoetangium* in the presence of lateral gametoecia. *Pleurochaete* does not have close morphological relationship with *Pseudosymblypharis* or the genera close to *Tortella* because of the lateral stalked perichaetia and perigonia as well as the restriction of the distinctive marginal border to the edge of the leaf, the relatively small, thick-walled proximal leaf cells gradually intergrading with the distal laminal cells. The marginal band of elongate, vesiculose cells also tends to become narrowed as it approaches the leaf insertion, sometimes becoming only one or two cells wide from a width of up to 10 cells.

1. *Pleurochaete luteola* (Bescherelle) Thériot,
Smithsonian Misc. Collect. 78(2): 14. 1926 [F]



Trichostomum luteolum Bescherelle,
Mém. Soc. Natl. Sci. Nat.
Cherbourg 16: 178. 1872

Cauline leaves (2–)3–4.5 mm; basal hyaline marginal band regularly sharply and irregularly denticulate distally, extending $\frac{1}{2}$ – $\frac{3}{4}$ the length of the leaf, evident on leaves on dry stems as a shining,

undulate area above the edge of the subtending leaf, depauperate stems with leaves to 2 mm show the hyaline band to at least $\frac{1}{4}$ the leaf length, and usually on some leaves nearly $\frac{1}{2}$; hyaline cells of band smooth distally, the cells elongate and becoming short-rectangular distally; longest median basal cells 7–10:1; median laminal cells ca. 7 μ m wide, quadrate.

Not fruiting in the flora area. Exposed clay or sandy soil over calcareous rock, especially in cedar barrens or glades, dry bluffs, ledges; low to moderate elevations; Ala., Ariz., Ga., Miss., Mo., N.Mex., Okla., Tenn., Tex.,

Va.; Mexico; West Indies (Cuba, Dominican Republic, Haiti); Central America (Guatemala); South America (Colombia, Ecuador, Peru).

The length of the limb does not generally correlate with stem robustness or leaf length, as discussed by various authors, such as E. B. Bartram (1949), although it is naturally shorter in depauperate material, extensively displayed in Texas specimens with stems and leaves of low stature. Undulations in the leaf base proximal to the limb may give the appearance of a leaf shoulder, but there is no abrupt narrowing of the leaf in this region, as there is in *Pseudosymblypharis*, which narrows abruptly here, forming a shoulder above the clasping leaf base. Both genera display porose basal cells, near the costa, but in *Pleurochaete* this feature is not as conspicuous. In Texas, both definitive *P. luteola* and large series of depauperate specimens occur. The latter were all in exposed situations on open soil, and the limb did indeed relatively short on these very short-stemmed and short-leaved specimens ($\frac{1}{4}$ – $\frac{1}{2}$ the leaf length). Still, these specimens, although the most reduced in typical New World characters, have stronger borders than typical material of *P. squarrosa* from the Old World.

7. **TORTELLA** (Lindberg) Limpricht, Laubm. Deutschl. 1: 599. 1888, name conserved
• [Latin *tortus*, twisted, and *-ella*, diminutive, alluding to peristome teeth]

Patricia M. Eckel

Mollia subgen. *Tortella* Lindberg, Musc. Scand., 21. 1879

Plants small to medium-sized, in loose or dense tufts, mats or compact sods, fragile, dull green, yellowish to dark green distally, black, brown or tan proximally with prominent shining costae. **Stems** erect, often branched, in transverse section with hyalodermis, somewhat weak sclerodermis, central strand absent or present, rhizoids dense or few at the base, occasionally tomentose; axillary hairs long, 1-seriate, of 10–20 cells, hyaline. **Stem leaves** cirrhate-crispate to incurved when dry, spreading to recurved when moist, elongate-oblong to linear-lanceolate or linear-subulate, widest at or near the base; base hyaline, oblong, erect; margins plane to incurved distally, generally entire and minutely crenulate by projecting papillae, but often slightly or irregularly scalloped by indentations at points of laminal weakness, occasionally somewhat to strongly undulate, rarely with a border of elongate, clear, smooth cells in one series beyond midleaf, gradually tapering distally or more or less abruptly narrowed; apex acute or obtuse, cucullate or concave, with an apiculus, mucro or short subula; costa strong, percurrent to short-excurrent, adaxial and abaxial epidermal cells often present, often interrupted, adaxial and abaxial stereid bands and 1 layer of median guide cells present, hydroid strand occasionally present; proximal cells enlarged, laxly long-rectangular, thin-walled, hyaline, occasionally brown and rather thick-walled, smooth, abruptly differentiated from the green cells distally or gradual in transition, limit of the proximal region usually appears as a V, sometimes a U, often extending

distally up each leaf margin as a short or elongated border; distal laminal cells medially and distally rounded-hexagonal, chlorophyllose, frequently obscured by numerous, dense, C-shaped papillae on both surfaces. **Specialized asexual reproduction** at the stem apex occasional, by deciduous or fragile propaguloid leaf tips, or by deterioration of fragile leaves along zones of laminal weakness. **Sexual condition** dioicous, occasionally autoicous; perigonia terminal, short-foliose to gemmate or as stalked buds in leaf axils of perichaetiate plants; perichaetia terminal, leaves not or little differentiated, or distinct and long-setaceous. **Seta** 1(–2) per perichaetium, yellow or reddish proximally with age, to 3 cm, erect, smooth. **Capsule** erect and symmetric or slightly inclined, yellow to reddish brown, darker red or brown at mouth, elliptic to cylindric, more or less wrinkled-plicate when dry and empty; annulus sometimes present, of 1–4 rows of vesiculose cells, persistent; operculum conic or long-rostrate, half as long as the urn or longer, straight or inclined; peristome orange-red, single, with a low basal membrane, of 32 filiform rami joined at the base into 16 pairs, twisted counterclockwise or merely obliquely inclined, branched-spiculose, rarely nearly smooth. **Calyptra** cucullate, smooth. **Spores** 8–12(–20) μm , yellowish brown, moderately coarsely to finely papillose to nearly smooth.

Species 53 (7 in the flora): nearly worldwide.

Trichostomum is similar to *Tortella* in leaf shape and margin flexion, but has distal laminal cells differentiated from the proximal cells in a line straight across the leaf base or in a low, poorly defined U shape, i.e., straight across but with some smooth, hyaline, elongated proximal cells extending up the leaf margins distal to the leaf shoulder. The proximal-cell line of differentiation usually forms a distinct V shape in *Tortella*. The peristomes of *Trichostomum* are erect, often short and frequently smooth, whereas those of *Tortella* are long and twisted generally 2–3 times (only slightly so in *T. flavovirens*) and densely spiculose in noncleistocarpous species (see R. H. Zander 1993). In much of the literature the peristomes of *Tortella* are described as papillose, when they are actually spiculose.

Pleurochaete does not have the V-shaped area of differentiated hyaline proximal echlorophyllose cells as with *Tortella*, but has a median area of gradually differentiated proximal cells and a strong border of several rows of cells contrasting with both laminal and proximal cells in being abruptly longer, thinner-walled, smooth and without chlorophyll. *Pleurochaete* also has perichaetia, in addition to perigonia, borne laterally on short branches on the main axis of the plant.

Species in *Weissia* are similar to *Tortella* by the incurving leaf margins (generally strongly and sharply incurved throughout the leaf length) with a tendency toward cucullation in the leaf apex. The proximal cells of some *Weissia* species may extend slightly up the margins, as in species of *Trichostomum*, and most especially, *Weissia jamaicensis* resembles a *Tortella* by a proximal region with a V shape. In the following treatment, great emphasis has been put on the cross section of the distal region of the leaf in delimiting taxa and for discussing relationships.

SELECTED REFERENCES Crundwell, A. C. and E. Nyholm. 1962. Notes on the genus *Tortella*. I. *T. inclinata*, *T. densa*, *T. flavovirens* and *T. glareicola*. Trans. Brit. Bryol. Soc. 4: 187–193. Eckel, P. M. 1998. Re-evaluation of *Tortella* (Musci, Pottiaceae) in conterminous U.S.A. and Canada with a treatment of the European species *Tortella nitida*. Bull. Buffalo Soc. Nat. Sci. 36: 117–191. Haring, I. M. 1938. *Tortella*. In: A. J. Grout. 1928–1940. Moss Flora of North America, North of Mexico. 3 vols. in 12 parts. Newfane, Vt. and New York. Vol. 1, pp. 165–170.

1. Leaves oblong-lanceolate or elliptical, apex broadly acute to obtuse, sometimes cucullate.
 2. Autoicous, nearly always fruiting; distal margins plane to erect, apex broadly acute; distal leaf cells about 6–7 μm ; central strand present; cells on adaxial surface of the costa quadrate and papillose throughout most of its length; stems short; plants typically rosulate, densely foliose 1. *Tortella humilis*
 2. Dioicous, seldom fruiting; distal margins incurved to strongly or variably cucullate at the apex, apex obtuse; distal leaf cells 7–11(–14) μm ; central strand present or absent; cells on adaxial surface of the costa quadrate and papillose throughout most of their length or mostly or entirely elongate and smooth; stems elongate; plants loosely foliose.
 3. Stem central strand present; costa with adaxial epidermis: areas on the adaxial surface of the costa with quadrate papillose cells; leaf apex variably somewhat cucullate, acute or obtuse with apical margins incurved; leaves flat in the leaf middle, keeled distally; fertile perichaetial leaves not much differentiated; mosses exclusively of coastal North Carolina south to Florida and west to Texas . . . 2. *Tortella flavovirens*
 3. Stem central strand absent; costa without adaxial epidermis: adaxial surface of the costa with smooth, elongate cells throughout the leaf length; leaf apex distinctly cucullate, occasionally acute, leaves tubulose; fertile perichaetial leaves conspicuously differentiated, with subulate tips; mosses of the Great Lakes region and north.
 4. Leaf cells 11–12 μm or less, stems orange to greenish yellow-brown, leaves deep yellow or orange in KOH; leaves irregularly or uniformly twisted on the stem; leaf apices usually cucullate to narrowly acute, not deciduous; leaves in section usually keeled at the costa, margins incurved; rock crevices or unconsolidated alluvial sediments near water 6. *Tortella inclinata*
 4. Leaf cells averaging 14 μm ; stems dark green to brown, leaves green in KOH; leaves erect, twisted only at the stem tips; leaf apices variable, usually acute to acuminate, never uniformly cucullate, frequently with a narrowed apical deciduous point; leaves in section broadly tubulose; limestone pavements with thin soil cover in the Great Lakes region 7. *Tortella rigens* (in part)
1. Leaves narrowly short to long- or linear-lanceolate, not cucullate or obtuse, apex narrowly acute, tapering to an acuminate point, sometimes apex very long, with a long, setaceous point.
 5. Leaves with distinctive apical propaguloid modifications, leaf apices regularly fallen.
 6. Stems 1–5 cm, coarsely tomentose; central strand absent; distal leaves to 7 mm, densely crowded, rigid, with patches of elongated, nonpapillose cells on distal leaf margins of young leaves at the stem apex; leaf cells 10–12 μm ; lamina proximal to subula 2-stratose; apical propagula falling in a single rigid unit; subulate limb 2- to multistratose 5. *Tortella fragilis*
 6. Stems 0.5 to 1.5 cm, scarcely or not tomentose; central strand present; distal leaves 1.5–2 mm, sparse, soft, leaf tips without differentiated marginal cells; leaf cells 14 μm ; lamina 1-stratose throughout; propaguloid leaves and apical propagula articulated by periodic constrictions, falling in several pieces; leaves 2-stratose only in patches or along costa distally 3. *Tortella alpicola* (in part)
 5. Leaves without apical propaguloid modifications although some apices may be somewhat fragile.
 7. Stems with central strand, leaf cells ca. 14 μm 3. *Tortella alpicola* (in part)
 7. Stems without central strand, or this rare, leaf cells to 14 μm but often less.
 8. Leaves tubulose, margins broadly incurved; most distal laminal cells 14 μm ; quadrate, papillose adaxial cells on the surface of the costa absent throughout the leaf length to a width of two or three cells in section; leaf apices deciduous; limestone pavements in the Great Lakes region 7. *Tortella rigens* (in part)
 8. Leaves plane to canaliculate, margins plane to erect; distal laminal cells seldom attaining 12 μm , usually less; quadrate, papillose adaxial cells on the surface of the costa present in the median leaf region or higher; of general temperate to Arctic distribution 4. *Tortella tortuosa*

1. *Tortella humilis* (Hedwig) Jennings, Man. Mosses W. Pennsylvania, 96. 1913



Barbula humilis Hedwig, Sp. Musc. Frond., 116, plate 25, figs. 1–4. 1801; *B. caespitosa* Schwägrichen; *Tortella caespitosa* (Schwägrichen) Limpricht

Plants usually dull and dark green to sordid yellow-green distally, brown to black proximally, typically compact and rosulate to

more elongate and showing annual whorls. **Stems** almost absent or stems to 0.5(–0.7) cm, central strand distinct, densely radiculose with red-brown radicles or infrequently populations with elongate stems without tomentum. **Stem leaves** densely foliose in rosulate habits, abruptly larger distally, the whorl-bases consisting of small leaves, loosely and variously incurled and contorted, occasionally somewhat crisped when dry, widespreading to patent when moist, typically oblong or oblong-spathulate, most leaves flat at mid leaf, somewhat concave and weakly keeled near the apex, not cucullate; 1.5–3.5 (–4) mm; base sub-clasping and often appearing narrower than the limb to somewhat broader and elliptic; margins flat to weakly and broadly undulate, erect or broadly incurved near the apex; apex typically obtuse to broadly or occasionally narrowly acute, usually stoutly mucronate; costa short-excurrent, adaxial surface papillose, adaxial epidermal cells typically quadrate to short-rectangular and similar to the laminal cells throughout, sometimes smooth and narrowly elongate cells (8:1) toward the apex due to exposure of the stereid band or, in the extreme apex, exposure of the guide cells; in cross section adaxial epidermis present, often interrupted in the extreme distal portion of the leaf, proximal laminal cells yellow-hyaline, elongate, laxly thin-walled, gradually distally papillose, marginal basal cells longer and larger than median cells, occasionally approximating a band of differentiated cells; proximal cells interior to the marginal gradually differentiated from the distal laminal cells; distal laminal cells small, typically 6–7(–9) μm wide. **Specialized asexual reproduction** none. **Sexual condition** autoicous; perigonia small, distinctive, stalked, flattened, usually single, rarely geminate, frequently yellow or orange, foliose buds of 2–6 leaves in axils of the distal leaves alongside and proximal to the perichaetium; inner perichaetial leaves little differentiated from stem leaves. **Seta** about (0.5–)0.7–1.7 cm; one per perichaetium, but often three to four per plant from different branches. **Capsule** 1.5–3 mm; annulus

deciduous in fragments; operculum 1.2–1.5 mm; peristome teeth, to over 1 mm, spirally wound 2 or 3 times.

Capsules mature spring. *Thuja* swamps and bogs, near streams, hard and softwood forests, dry, exposed or moist and shaded stations, bark at the base of trees, acid or basic substrates, rock crevices and surfaces, sandy or humic soil, organic debris, mortar and brick, concrete, maritime and inland forests; low to moderate elevations; B.C., N.S., Ont., Que.; Ala., Ariz., Ark., Conn., Del., Fla., Ga., Ill., Ind., Iowa, Kans., Ky., La., Md., Mich., Minn., Miss., Mo., Nebr., N.J., N.Y., N.C., Ohio, Okla., Pa., S.C., Tenn., Tex., Vt., Va., Wash., W.Va., Wis.; Mexico; West Indies; South America; Europe; Asia; Africa; Pacific Islands.

Uniquely among species of the genus in the flora area, except for var. *arctica* of *Tortella tortuosa*, in *T. humilis* the proximal laminal cells of the leaf are typically gradually differentiated from the distal cells with a zone of cells intermediate in color, cell size, cell wall thickness and papillosity, the angle of hyaline marginal cell differentiation typically shallow across the leaf base, then extending up the margins in a U shape. This character is typical of the genus *Trichostomum*, with which *Tortella* is closely allied. Small (depauperate) plants of *T. flavovirens* may share this character. Typical basal cell differentiation in *Tortella* is abrupt, the angle of differentiated cells steep, the proximal echlorophyllose and distal chlorophyllose cell boundary sharp.

In cross section, the costa of *Tortella humilis* diminishes in size toward the leaf tip: sectioning distally along the leaf, the epidermal layer first disappears, leaving up to two stereid cells in width exposed. In some instances at the extreme apex, even the stereid layer disappears leaving the guide cells exposed. The well-developed peristome—elongate and conspicuously twisted—will distinguish *Tortella humilis* from specimens of *T. flavovirens* and *Trichostomum* species, whose peristomes are either not or little twisted, or are rudimentary. Any specimen without fruit is unlikely to be *Tortella humilis*. H. A. Crum and L. E. Anderson (1981) well described and illustrated the rare species *Trichostomum spirale* from the Great Lakes region (Ontario, Wisconsin, Minnesota) that, like *Tortella humilis*, is a nearly stemless plant with gradually differentiated proximal cells and a similar leaf shape. It also has stalked perigonial buds and is autoicous. It may be distinguished by the peristome teeth said to be short, erect and smooth or marked with spiral lines rather than spiculate papillae, the latter characteristic of peristomes of the genus *Tortella*.

2. *Tortella flavovirens* (Bruch) Brotherus in H. G. A. Engler and K. Prantl, Nat. Pflanzenfam. 214[I,3]: 397. 1902



Trichostomum flavovirens Bruch, Flora 12: 404, plate 2, fig. 7. 1829

Plants usually pale delicate yellow distally, yellow-brown proximally, elongate, not rosulate, annual whorls often evident. **Stems** 0.3–1 cm, hyalodermis large, sclerodermis inconspicuous, cells of central cylinder thick-walled, central strand present, without tomentum, rhizoids thick and sparse at the base. **Stem leaves** loosely foliose, gradually somewhat larger and more crowded toward the stem tips, loosely to typically tightly incurled-contorted around the stem when dry, suberect to spreading when moist, oblong-ovate or ovate-lanceolate, strongly keeled-concave distally, medially flat to broadly channeled across the leaf proximally, 2–3.5 mm; base somewhat broader, elliptical; margins erect to incurved-involute, especially toward the apex, not or somewhat undulate, limb gradually or quickly narrowed; apex obtuse, subcucullate; costa percurrent or short-excurrent, rarely disappearing before the apex on some leaves, adaxial epidermal cells papillose-quadrate to short-rectangular at midleaf, frequently disappearing, showing smooth and narrowly elongate (6:1) stereid adaxial cells at the extreme apex; in cross section adaxial epidermis of quadrate, papillose cells typically present, occasionally absent in patches toward the apex, proximal laminal cells in larger leaves rather abruptly differentiated from distal cells, yellow-hyaline and nearly concolorous with the distal lamina, long-rectangular, 8(–9):1, laxly thin-walled, rather gradually papillose; distal laminal cells 10–12 (–14) μm wide. **Specialized asexual reproduction** none. **Sexual condition** dioicous; perigonia not seen; perichaetial leaves little differentiated from stem leaves. **Seta** 1.1–1.3 cm. **Capsule** 1.8–2.2 mm, annulus none; operculum 0.75–1 mm, nearly subulate when young, more broadly long-conic just before dehiscence; peristome teeth relatively short, to 0.5 mm, straight or obliquely inclined and slightly twisted, especially when newly deoperculate.

Capsules rare, mature mid to late spring. Salt-tolerant, near tidal zone in saltwater spray on coastal beaches and offshore islands, exposed sites on sandy soil, coquina, among dunes, juniper scrub, lawns and other grassy, weedy areas, damp concrete, mortar in old forts; near sea level; Ala., Fla., Ga., N.C., S.C., Tex.; Bermuda; Europe; Asia (Syria); n Africa; Atlantic Islands (Macaronesia); Pacific Islands (New Zealand).

In the United States, all specimens named *Tortella flavovirens* that were collected inland from coastal habitats were redetermined to be some other species: most frequently *T. humilis*, *Trichostomum crispulum*, and *Weissia* species. The leaf cross section of *Tortella flavovirens* exhibits an adaxial layer of quadrate, papillose cells across its surface throughout the leaf length excepting the proximal region and the extreme apex. The peristome of *Tortella flavovirens* is somewhat short, but not rudimentary. It is erect or somewhat inclined and reminiscent of *Trichostomum* peristomes, which are smooth, papillose or striolate and generally erect. Sterile *Weissia* species may be confused with *T. flavovirens*, being pale yellow with the same cell size, and appearing to have a cucullate apex with the marginal basal cells somewhat extending up the leaf: these will, however, have no basal marginal extension on some leaves and the distal leaf margins will be tightly inrolled or incurved to a stronger degree than in any *Tortella* species; the substrate is frequently inappropriate in these specimens, such as bark at the base of trees or some other woody or humic substrate, likewise inland stations. *Trichostomum crispulum*, with which *Tortella flavovirens* has occasionally been confused, has smaller leaf cells, a broader, chestnut-colored costa and has a U-shaped proximal differentiated area of cells in all leaves. A. J. E. Smith (1978) recorded *T. flavovirens* var. *glareicola* (Christensen) Crundwell & Hyholm from Canada, most likely based on the citation by A. C. Crundwell and E. Nyholm (1962) of a depauperate specimen from Alberta (C. D. Bird 3624), identified by Bird as *T. tortuosa*. These plants “with longly tapering acutely pointed leaves” may be one of the peculiar instances of depauperate, large-celled *T. tortuosa* specimens (see discussion under that species). R. R. Ireland et al. (1987) considered var. *glareicola* to be absent from Canada, while L. E. Anderson et al. (1990) excluded it from North America.

3. *Tortella alpicola* Dixon, Ann. Bryol. 3: 54. 1929



Tortella fragilis var. *tortelloides* (S. W. Greene) R. H. Zander & Hoe; *T. tortelloides* (S. W. Greene) H. Robinson

Plants light or dark and vivid or clear green distally, pale buff-brown proximally with glistening white leaf bases, elongate, not rosulate. **Stems** thin, slender, 0.5–1(–1.5) cm, branches few to several, central strand present and conspicuous, not tomentose except in perichaetiate plants. **Stem leaves** fragile, closely to loosely aggregated, uniform in size, apices in sterile plants (except the

youngest) usually fallen, incurved-circinate and weakly contorted when dry, erect-spreading, occasionally patent when moist, gradually long-lanceolate, 1.5–2 mm; base undifferentiated or somewhat broader than the limb, elliptical; margins of some leaves weakly undulate, constricted, lobed in scallop-shapes in several places distally, erect to incurved; apex narrowly acuminate, occasionally sharply contracted into a subula in the apical $\frac{1}{3}$, this a papillose cylinder about the size of the costa, composed of a series of barrel-shaped segments disarticulating at constrictions, intact subula and tip of propaguloid apex with an apiculus of several cells, this usually dentate and tipped by one or two, elongate, sharply pointed clear cells, in sterile plants leaf apices caducous along zones of weakness; costa short-excurrent, in leaves of fertile plants adaxial surface covered distally by an epidermis of quadrate, papillose laminal cells, back of the costa smooth throughout—in leaves of fragile sterile plants abaxial costa surface smooth only proximally apical subula, densely papillose on both adaxial and abaxial surfaces in the distal subulate region, in cross section cells weakly differentiated and frequently rather chaotic, adaxial epidermis always present, adaxial stereid cells often disappearing in the distal region of the leaf, proximal laminal cells abruptly differentiated from distal cells, pale white-hyaline and transparent; distal laminal cells relatively large, 10–14 μm wide, lamina 1-stratose but apparently 2-stratose at juncture of lamina and costa, especially along the distal costa in propaguloid leaves of sterile plants; marginal cells undifferentiated, papillose-crenulate throughout. **Specialized asexual reproduction** in two modes, a general fragility of the leaf lamina as well as smaller, soft, multistratose, propaguloid deciduous leaf apices articulated by regular constrictions, falling early in units of approximately uniform length. **Sexual condition** apparently dioicous; perigonia not seen; perichaetiate stems tomentose, perichaetia terminal on successive perichaetial innovations; outer perichaetial leaves differentiated, especially evident when dry, longer than the cauline leaves, long-lanceolate to linear-lanceolate, fragile, tipped with long, rigid, subulate, smooth awns; rising beyond the contorted stem leaves when dry, not propaguloid, unbordered. **Sporophytes** unknown.

Shaded or exposed, wet or dry rocks, crevices and ledges of granite, quartzite, schist, sandstone and calcareous outcrops on cliffs and in canyons, cracks in a limestone gully, cavern, wet, mesic tundra, wet log, dry limestone cliff face; low to high elevations (20–3300 m); Alta., N.W.T., Que., Yukon; Alaska, Ariz., Calif., Colo., Idaho, Mont., Nebr., Utah, Wyo.; South America (Colombia); Asia (India); Pacific Islands (Hawaii); Antarctica (Alexandra Island).

Tortella alpicola is associated with a western corridor of both montane and valley habitats, including the western Great Plains, extending in an arc from Arizona to Ellesmere Island. It is the smallest of the North American *Tortellae*. The plants are noted by their small size, absence of tomentum on typical (sterile) stems, broken tips on most of the leaves, vividly shining white leaf bases on the stem in contrast with the deep or bright green of the limb, and large leaf cells (to 14 μm wide). Small fertile plants of *T. tortuosa* and *T. inclinata* have a similar aspect; these also have stiff, awned perichaetial leaves distinct from the cauline leaves. The large leaf cells and presence of a distinct stem central strand in *T. alpicola* will differentiate ambiguous specimens from similarly small stems of *T. tortuosa* and *T. fragilis*. The costal anatomy of leaves of *T. alpicola* shows two sets of characteristics, one for sterile plants and one for fertile (perichaetiate). In sterile plants, the costal layers (epidermis, stereids and guide cells) are weakly differentiated and in many cases, not differentiated at all; the costa is undifferentiated in the proximal part of the leaf where the laminae are fully extended and 1-stratose. The laminae are never fully 2-stratose but occasionally exhibit 2-stratose patches. In sterile plants, the epidermal and guide cell layers may be chlorophyllose and there are papillae on the abaxial surface of the costa. In *T. fragilis*, the costal cells become undifferentiated in the nonlaminar subula while the lamina just proximal to the propagulum is 2-stratose.

In sterile plants the abaxial stereid band disappears along with the other layers. In perichaetiate plants the abaxial and adaxial stereid bands are definite, with thick-walled cells. The adaxial stereid layer, however, appears to quickly disappear in the distal region of the leaf, rather than the epidermal layer, the reverse of every *Tortella* species in North America (excepting many specimens of *T. tortuosa* var. *fragilifolia*). The two other *Tortella* species in North America with stem central strands, *T. humilis* and *T. flavovirens*, have two well-differentiated, strong stereid bands abaxial and adaxial to the guide cell layer. The propaguloid modifications of the leaves are different in kind between *T. fragilis* and *T. alpicola*. The propagules of the former species fall as a single unit from leaves disposed all along the stem, whereas those of the latter fall in numerous, fragile, barrel-shaped caducous units of about equal length from the leaf apices.

SELECTED REFERENCE Eckel, P. M. 1997. The moss *Tortella alpicola* Dix. new to Alberta and the Yukon Territory with a discussion of its range and comments on related species. *Canad. Field-Naturalist* 111: 320–322.

4. *Tortella tortuosa* (Hedwig) Limpricht, Laubm.
 Deuschl. 1: 604. 1888 [F]



Tortula tortuosa Hedwig, Sp.
 Musc. Frond., 124. 1801

Plants dull, green, yellow-green or yellow-brown distally, brown proximally, becoming reddish at higher latitudes and altitudes, elongate. **Stems** 1–6 cm, leaves distantly disposed along the stem with the shining leaf bases usually

apparent, central strand nearly always absent, rarely present, sclerodermis moderately developed, 2–3(–4) cells deep, cells of the central cylinder rather thick-walled, stems visibly tomentose with dense red-brown radicles, rarely nearly eradiclese in very small stems. **Stem leaves** rather soft, uniform in size, strongly crisped or contorted with spirally curled tips when dry, flexuose- to widespreading when moist, long-lanceolate to linear-lanceolate, broadly to narrowly concave or nearly plane proximally to more or less keeled in the apical region, (2–)3–6.5(–7) mm; base somewhat broader than limb, oblong; margins usually shortly and strongly undulate, evenly crenulate-papillose, gradually subulate-acuminate, apex acumination confluent with the mucro, leaves at the extreme stem apex surmounted by a stout, multicellular mucro; costa excurrent as a long, smooth or denticulate mucro or short awn, usually composed of 5–10 rhomboidal cells, adaxial cells of the costa variable, costa distal to the leaf base to the distal median region covered by an epidermis of quadrate to short-rectangular (2:1) papillose cells, in the distal adaxial region variously with a narrow or broader central groove of exposed, smooth, elongate (8:1) stereid cells, occasionally the groove conspicuous and extensive; proximal laminal cells abruptly differentiated from distal cells, hyaline, laxly thin-walled; distal laminal cells 1-stratose, quadrate, 7–10(–13) μm wide, marginal cells undifferentiated. **Specialized asexual reproduction** none except possibly through fragility of the lamina in some populations, or weakness toward the apex. **Sexual condition** dioicous, but seldom fruiting; perigoniate plants rare; perigonia apparently few per stem, inner perigonial bracts ovate and abruptly apiculate, scarcely longer than the antheridia, 0.5 mm; perichaetiate plants common; perichaetia numerous on the stem; perichaetial leaves differentiated even in unfertilized perichaetia, slender and erect at the base, long, 5–5.5 mm, somewhat sheathing, distal part, consisting mostly of costa, setaceous-subulate, erect, in fertile plants, stiff and slightly flexuose, distinct and conspicuous above the tightly crisped cauline leaves

when dry. **Seta** 0.9–2.7(–3.5) cm. **Capsule** 1.5–3.3 mm; annulus not vesiculose; operculum 1.5–2 mm; peristome teeth long and spirally wound 2 or 3 times, 1.1–1.4 mm.

Varieties ca. 20 (3 in the flora): North America, Mexico, Central America, Europe, Asia, n Africa, Atlantic Islands (Iceland).

1. Plants red-green, appearing black proximally, densely foliose with a thick apical coma, leaf bases hidden; stems appearing atomentose but tomentum hidden in the bases of branch innovations; leaves not fragile, intact; leaves often strongly squarrose-recurved when wet, plane, not undulate; proximal laminal cells thick-walled and brownish, intergrading in shape and size with the distal cells, which are often nonpapillose in the area of merger; leaves broadly concave in section; costa at midleaf exposed adaxially by as much as four stereid cells 4b. *Tortella tortuosa* var. *arctica*
1. Plants green or yellow-green, appearing brown proximally, loosely foliose, some leaf bases exposed, only slightly comose at stem apex; stems conspicuously tomentose; leaves fragile or not, erect- to erect-spreading when wet; undulate or plane; proximal laminal cells thin-walled and hyaline, sharply differentiated in shape and size from the papillose distal cells, which are papillose in the area of contact; leaves keeled in section, costa in apical region exposed adaxially by up to 2 stereid cells in width or completely covered with an adaxial epidermis of quadrate papillose cells.
2. Leaves in tight, complex spirals when dry, appearing soft or lax throughout the stem length, not fragile or erose, leaf tips nearly all present; conspicuously undulate; leaf cross section without 2-stratose areas beside the costa, the lamina uniformly 1-stratose, lamina intact, the costa always differentiated into guide cells, stereids and epidermal cells, adaxial stereid layer never disappearing toward the apex, adaxial epidermal layer typically absent apically in a medial groove to two stereid cells in width 4a. *Tortella tortuosa* var. *tortuosa*
2. Leaves in loose, simple spirals or once circinate when dry, appearing firm or rigid, often fragile and erose, leaf tips often absent; inconspicuously undulate, especially when dry; leaf cross section with 2-stratose areas beside the costa, the lamina irregularly 2-stratose in patches, lamina tattered, costa occasionally appearing undifferentiated in apical region of the leaf, adaxial stereid layer occasionally disappearing toward the apex, epidermal layer may be continuous throughout the leaf length 4c. *Tortella tortuosa* var. *fragilifolia*

4a. *Tortella tortuosa* (Hedwig) Limpricht var. *tortuosa*



Plants green or yellow-green, appearing brown proximally, loosely foliose, some leaf bases exposed, only slightly comose at stem apex. **Stems** conspicuously tomentose. **Leaves** in tight, complex spirals when dry, appearing soft or lax throughout the stem length, not fragile or

erose, leaf tips nearly all present; conspicuously undulate, fragile or not, erect- to erect-spreading when wet; undulate or plane; proximal laminal cells thin-walled and hyaline, sharply differentiated in shape and size from the papillose distal cells, which are papillose in the area of contact; leaves keeled in section, costa in apical region exposed adaxially by up to two stereid cells in width or completely covered with an adaxial epidermis of quadrate papillose cells; leaf cross section in one layer beside the costa, the lamina uniformly 1-stratose, lamina intact, the costa always differentiated into guide cells, stereids and epidermal cells, adaxial stereid layer never disappearing toward the apex, adaxial epidermal layer typically absent apically in a medial groove to two stereid cells in width.

Capsules mature late spring–summer (Jun–Aug). Calcareous regions, exposed or forest-shaded rock crevices, boulders, ledges of mountains or low, peaty soil and rotten wood, dry wooded hillsides or wet areas such as *Thuja* swamps, banks of streams over humus, river margins, northern regions in wet tundra and solifluction lobes; low to high elevations (100–3800 m); Greenland; Alta., B.C., N.B., Nfld. and Labr. (Nfld.), N.W.T., N.S., Nunavut, Ont., Que., Sask., Yukon; Alaska, Calif., Colo., Idaho, Ill., Ind., Iowa, Maine, Mass., Mich., Minn., Mont., Nebr., Nev., N.H., N.Mex., N.Y., N.C., Ohio, Oreg., Pa., S.Dak., Tenn., Tex., Utah, Vt., Va., Wash., Wis., Wyo.; Mexico; Central America (Guatemala); Europe; Asia; n Africa; Atlantic Islands (Iceland).

Variety *tortuosa* is striking in its crisped leaves in spirals when dry, which, together with the strongly undulate margins, is a trait absent in other species in the genus or related genera. The long, multicellular, vitreous awn confluent with the lamina is also distinctive. Only in the case of very depauperate forms is var. *tortuosa* confused with *Tortella fragilis*, which has leaves more rigid, more or less erect, not or only slightly contorted when dry and regularly fragile with propaguloid modifications in the leaf apex. Occasional specimens of var. *tortuosa* have large laminal cells, on average 12 μm wide and attaining 14 μm in individual cells. The leaves never have incurved margins nor are they apically cucullate as in *T. inclinata* or in the younger leaves of *T. rigens*. Throughout the range of var. *tortuosa* occasional puzzling specimens may be found with cell sizes to 14 μm in the distal region of the leaves (Nebraska, Alberta, Arctic specimens). Absence

of adaxial epidermal cells on the costa throughout much of the distal portion of the leaf may suggest *T. inclinata* in the loose sense, but epidermal cells may be found at least in the mid-proximal regions of most leaves. Occasional specimens determined as *T. fragilis* are richly perichaetiate specimens of *T. tortuosa* with extremely long perichaetial leaves throughout the stem resembling the subulate propagula at the leaf apices of the former species. The tips of these leaves, however, are not swollen at the distal ends.

Variety *tortuosa* exceptionally has a distinct central strand but this trait is generally absent. *Trichostomum tenuirostre*, with leaves also spirally twisted when dry, has hyaline proximal cells that extend indistinctly only a short way up the margin by a few cells in width, and the stem is not radulose. *Trichostomum tenuirostre* usually has a large and distinct stem central strand, and the apex of the leaf often has low and distant teeth.

4b. *Tortella tortuosa* var. *arctica* (Arnold) Brotherus in B. A. Fedtschenko, Fl. Aziat. Ross. 13: 160. 1918



Mollia tortuosa var. *arctica* Arnold, Ark. Bot. 13: 51. 1913; *Tortella arctica* (Arnold) Crundwell & Nyholm

Plants red-green, appearing black proximally, densely foliose with a thick apical coma, leaf bases hidden. **Stems** appearing atomentose but tomentum hidden in the

bases of branch innovations. **Leaves** densely disposed on stem or in dense annual whorls distinctly separated by less foliose regions, terminating in a thick multi-branched comal tuft, tips present and not fragile, intact; leaves often strongly squarrose-recurved when wet, plane, not undulate; proximal laminal cells thick-walled and brownish, intergrading in shape and size with the distal cells, which are often nonpapillose in the area of merger; leaves broadly concave in section; leaf cross section with cells in one layer beside the costa, the lamina uniformly 1-stratose; costa at midleaf exposed adaxially by as much as four stereid cells, the costa always differentiated into guide cells, stereids and epidermal cells, adaxial stereid layer never disappearing toward the apex, adaxial epidermal layer typically absent apically in a medial groove to 2 stereid cells in width.

Depressions in mesic to wet tundra, soil over limestone and sandstone, below snowfields, hillside and mountain seepage and seepage channels, bordering streams and ponds, wet rock surfaces, fens, wet frost boils, frequently on ridges in the wetter areas; *Carex-Eriophorum* meadows, *Dryas* communities, *Cassiope* heaths; wet sandy *Eriophorum triste* meadow; low to high elevations (0–3600 m); Greenland; B.C., Nfld. and Labr. (Nfld.), N.W.T., Nunavut, Yukon; Alaska, Colo., Maine; Asia (China, Russia in Siberia).