

A revision of *Pilotrichella* (Lembophyllaceae: Musci)

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Abstract. *Pilotrichella* (C. Müll.) Besch. is a predominantly epiphytic genus of six species found in Hawaii, the Neotropics and Africa: *P. cuspidans*, *P. flexilis*, *P. mascarenica*, *P. mauiensis*, *P. reesei*, *sp. nov.* and *P. vermiformis*, *sp. nov.* The sporophytic features of *Pilotrichella* are uniform throughout the genus. Gametophytic features of the genus that show significant variation include: 1. relative plant size; 2. branch bud shape; 3. leaf shape; 4. leaf margin stance; 5. extent of alar cell differentiation; 6. leaf apex shape; and 7. spore size. The section *Orthostichella* differs from *Pilotrichella*, in often having primary stolons as well as stipitate stems, smaller plants with spirally ranked leaves having sparsely developed alar cells and short double costae. The exostome teeth in *Orthostichella* are smooth to papillose while those of *Pilotrichella* are striate at base. *Orthostichella* is here considered distinct from *Pilotrichella* at the generic level. *Pilotrichella* is placed in the Lembophyllaceae rather than the Meteoriaceae on the basis of its absolutely ecostate leaves and green, yellowish red or brown coloration. Within the Lembophyllaceae *Pilotrichella* appears isolated by virtue of its lack of a stem central strand, absolutely ecostate leaves, and more reduced peristome. *Pilotrichella quitensis* is transferred to the genus *Pleurozium* (as *Pleurozium quitense*, *comb. nov.*). *Camptochaete arbuscula* is reported from Hawaii, and *Weymouthia mollis* is reported from Tahiti and the Falkland Islands.

Pilotrichella (C. Müll.) Besch. is a genus of predominantly epiphytic, frequently pendulous mosses of tropical and subtropical American-African distribution. Hedwig (1801) described the oldest species now placed in *Pilotrichella* (as *Leskea flexilis* Sw. ex Hedw.), but the species generally accepted in the genus were first brought together by Müller (1850) under *Neckera* Hedw. sect. *Pseudopilotrichum*. C. Müll. subsections *Orthostichella* C. Müll. and *Pilotrichella* C. Müll.

Bescherelle (1872) elevated Müller's subsect. *Pilotrichella* to generic rank. The newly established *Pilotrichella* was broadly conceived and included four sections: *Orthostichella* (C. Müll.) Besch., *Eupilotrichella* (C.

Müll.) Besch., *Papillaria* (C. Müll.) Besch., and *Meteoridium* (C. Müll.) Besch. *Papillaria* had previously been removed from this group by Lorentz (1864). Jaeger & Sauerbeck (1877) refined *Pilotrichella* by dividing it into two unranked groupings: *Eupilotrichella* (including Bescherelle's sect. *Meteoridium*) and *Orthostichella*. Section *Meteoridium* was removed from *Pilotrichella* by Brotherus (1906) who also positioned the genus (with sections *Orthostichella* and *Eupilotrichella*) in the tribe Meteorieae. This placement of *Pilotrichella* was followed by Fleischer (1908) who assigned the genus to the Meteoriaceae (tribe Pilotrichelleae). The association of *Pilotrichella* with the Meteoriaceae has been generally accepted (see e.g., Brotherus 1925, Bartram 1949, Florschütz 1964, Walther 1983, Vitt 1984, Spessard-Schueth 1994, Churchill & Linares 1995, Duarte-Bello 1997, Magill & van Rooy 1998, Gradstein et al. 2001).

The Meteoriaceae are usually placed in the Leucodontales (Fleischer 1908, Brotherus 1925, Walther 1983, Vitt 1984). The family, however, was transferred to the Hypnales by Buck (1994) and placed near the Brachytheciaceae in part because its exostome teeth are often horizontally striate at base and it lacks stolon-like primary stems that are tightly adherent to the substrate as well as greatly reduced stolon leaves. Buck (1994, 1994a) also reconsidered *Pilotrichella* and its systematic placement. As a result *Orthostichella* C. Müll. was resurrected as a genus (as *Pseudopilotrichum* (C. Müll.) Buck & Allen) and both genera along with *Weymouthia* Broth. and *Squamidium* (C. Müll.) Broth. transferred to the Lembophyllaceae.

There are a number of tropical and subtropical pleurocarpous genera that grow pendulous in predominately epiphytic habitats. These genera present classification problems because they appear to represent several phylogenetic lines as judged by their very different peristomial forms, but they exhibit considerable convergence in their gametophytic features. *Pilotrichella* is one of these problematic genera. It is difficult to decide if it belongs in the Meteoriaceae or Lembophyllaceae because its reduced peristome shows affinities to both families and it is hard to determine whether its gametophytic features are indicative of propinquity of descent or convergence. This situation is further complicated because the Meteoriaceae and Lembophyllaceae are so similar (e.g., compare the family descriptions of the Lembophyllaceae and Meteoriaceae in Buck & Goffinet 2000).

The leaves and stems of most genera placed in the Meteoriaceae often have parts that are intensely black. This odd feature is usually only noticed in passing, but it is so distinctive that when present one can immediately assign unknown specimens to the Meteoriaceae. Genera placed in the Lembophyllaceae can be green, yellowish red or brown, but they never exhibit this intense, at times shiny, black color. Furthermore, all of the genera now

placed in the Meteoriaceae that can produce this intense black coloration also have single costae. On the basis of these two features it appears that *Squamidium* should be returned to the Meteoriaceae. *Pilotrichella*, *Orthostichella*, and *Weymouthia* which are ecostate or have short double costae and a green, yellowish red or brown coloration seem properly placed in the Lembophyllaceae. Within the Lembophyllaceae *Pilotrichella* appears isolated by virtue of its lack of a stem central strand, absolutely ecostate leaves, and more reduced peristome.

As noted above *Orthostichella* is generally considered a section of *Pilotrichella*, but Müller (1879) used the name at the generic level as did Buck (1994, 1994a). *Orthostichella* differs significantly from *Pilotrichella* in its smaller plant size, and in often having primary stolons as well as stipitate stems. It also differs from *Pilotrichella* in having spirally ranked leaves with sparsely developed alar cells, and often its leaves have short double costae. Sporophytically *Orthostichella* differs from *Pilotrichella* in having shorter setae and smooth to papillose exostome teeth. Additionally the presence of large spores (to 64 μm) in *Pilotrichella* distinguishes the two taxa. For these reasons *Orthostichella* is here considered distinct from *Pilotrichella* at the generic level.

Pilotrichella is stable in most of its features. Its stolons, stems, and branches are identical in structure. It lacks a stem central strand, and its axillary hairs are usually reddish throughout. When the reddish coloration in the axillary hairs is weakly expressed it is the upper rather than the basal cells that remain colored. The stem and branch leaves of *Pilotrichella* are monomorphic, strongly concave, variously ovate in shape, and always lack a costa. Its entire to serrulate leaf margins are generally broadly incurved, and its linear-flexuose leaf cells are often strongly porose. The alar cells in *Pilotrichella* are well-developed, and occur as excavate groups of enlarged, reddish yellow, subquadrate to rectangular, porose cells. Gametophytic features of *Pilotrichella* that show significant variation include: 1. relative plant size; 2. branch bud shape; 3. leaf shape; 4. leaf margin stance; 5. extent of alar cell differentiation; 6. leaf apex shape; and 7. spore size.

The sporophytes of *Pilotrichella* are uniform throughout the genus. The setae are elongate and variously papillose roughened. The genus has ovoid to short-cylindrical capsules, long-rostrate opercula, and hairy, cucullate calyptrae. The *Pilotrichella* peristome is diplolepideous and reduced with yellowish white exostomes and endostomes that are nearly the same length as the exostome teeth. The more or less linear exostome teeth are lightly horizontally striate on the dorsal (outer) surface at base. The endostome has a low basal membrane with filamentous, narrowly perforated segments, and cilia are usually absent. Even though the *Pilotrichella* peristome is

significantly reduced in form, the presence at the base of the exostome teeth of horizontal striae indicates the peristome is basically hypnoid.

The name *Pilotrichella* combines the generic name *Pilotrichum* with the Latin substantival suffix *-ella* (diminutive).

Pilotrichella (C. Müll.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 222. 1872.

Neckera subsect. *Pilotrichella* C. Müll., Syn. Musc. Frond. 2: 129. 1850. Lectotype: *Leskea flexilis* Sw. ex Hedw. (designated here).

Pilotrichella sect. *Turgidella* C. Müll., Flora 82: 464. 1896, invalid name, no description. Type: *Meteorium mauiensis* Sull.

Pilotrichella sect. *Gastrella* C. Müll., Flora 82: 464. 1896, invalid name, no description. Type: *Pilotrichella desmoclada* C. Müll.

Pilotrichella sect. *Eupilotrichella* Besch. ex Broth., Nat. Pflanzenfam. 1(3): 811. 1906, illegitimate name (Art. 21.3, Greuter 2000).

Plants small, medium-sized or large, dull, light green, green, yellow-green, reddish yellow, or golden brown, in loose or stiff mats, often with pendent strands. Stem and branches in cross section with sclerodermis, firm-walled cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia absent, scale leaves present over branch buds. Primary stems creeping; rhizoids generally on the parts of the stems that touch the substrate, in circular clusters abaxially to the leaf insertions, dark red, smooth to finely roughened, mostly not branched; leaves smaller but not different in form or structure from secondary stem and branch leaves. Secondary stems arising irregularly from the primary stems, or primary stems transformed at the tips into secondary stems, often pendent, irregularly branched; axillary hairs numerous, all cells reddish, basal cells short, subquadrate, upper cells long-cylindrical; rhizoids absent. Secondary stem and branch buds short and swollen or narrowly elongate and terete. Leaves not ranked, erect-spreading, spreading or wide-spreading, (sometimes turgid) when dry, erect to erect-spreading when wet, concave, ovate, oblong-ovate, obovate, or ovate-deltoid, at times panduriform, somewhat clasping at base and variously auriculate; apices acute or acuminate, mucronate, cuspidate or hair-pointed, leaf tips reflexed or straight; margins broadly incurved above, at times meeting or overlapping at upper margins, entire below, serrulate (rarely entire) below the apex; costa absent; leaf cells linear-flexuose, porose at base, porose or occasionally straight-walled above, alar cells in bulging, excavate groups, subquadrate to short-rectangular, usually dark red or reddish orange. Branch and stem tips occasionally flagelliform, plants sometimes with slender branchlets having microphyllous leaves, or short branches with deciduous leaves. Dioicous. Perigonia gemmate, lateral on secondary stems and

branches, outer perigonia leaves clasping at base, squarrose recurved above, inner perigonia leaves broadly ovate, orange-red across the base; paraphyses and curved-cylindrical antheridia numerous. Perichaetia on short lateral branches; paraphyses and archegonia numerous; outer leaves clasping below, squarrose above, inner leaves sheathing, oblong-lanceolate, long-acuminate; vaginula of fertilized perichaetia densely hairy. Setae elongate, red, smooth below and papillose above or papillose roughened throughout. Capsules exerted, erect, ovoid to short-cylindrical; exothecial cells subquadrate to irregularly subrectangular, firm-walled; stomata superficial on neck; opercula long-rostrate; annuli rudimentary; peristome diplolepideous, yellowish white, exostome on dorsal (outer) surface lightly horizontally striate at base, finely papillose above, trabeculae weakly developed on both sides, endostome nearly as long as exostome, basal membrane low, segments filamentous, narrowly perforated, papillose, cilia rudimentary or absent. Calyptrae cucullate, densely hairy. Spores lightly roughened, oblong to rounded-triangular, 34–64 μm , or round, 18–28 μm .

1. Leaves ovate-deltoid, long-cuspidate to piliferous; branch buds narrow, elongate, and terete 1. *P. cuspidans*
1. Leaves oblong-ovate to broadly ovate, mucronate to cuspidate; branch buds short and swollen 2.
 2. Alar cells not restricted to an excavate group in the auriculate angle 5. *P. reesei*
 2. Alar cells more or less restricted to an excavate group in the auriculate angle 3.
3. Plants with slender branchlets having microphyllous leaves, or flagelliform branch tips, or deciduous leaves 4.
3. Plants without slender branchlets, flagelliform branch tips, or deciduous leaves 5.
 4. Leaves cuspidate, nearly all apices erect; slender branchlets with microphyllous leaves, flagelliform branch tips and/or deciduous leaves present 4. *P. maviensis*
 4. Leaves mucronate, most apices reflexed; plants only with deciduous leaves 2a. *P. flexilis* form *nudiramulosa*
5. Leaves cuspidate, nearly all apices erect 4. *P. maviensis*
5. Leaves mucronate or apiculate, most apices reflexed 6.
 6. Plants medium-sized to large, leaves 1.7–3.0 mm long 2. *P. flexilis*
 6. Plants small to medium-sized, leaves 1.2–1.6 mm long 7.

7. Leaves turgid when dry, often cochleariform, obtuse; upper leaf margins never overlapping 6. *P. vermiformis*
7. Leaves erect to erect-spreading when dry, oblong-ovate, broadly acute, upper leaf margins usually overlapping
..... 3. *P. mascarenica*

1. *Pilotrichella cuspidans* Ren. & Card., Bull. Soc. Roy. Bot. Belgique 29(1): 180. 1890. Protologue: Haiti. Haiti, Port au Prince, ad truncos arborum (Bertrand). Holotype: Haiti: Port au Prince, Leg. Bertrand, Herb. J. Cardot (PC). Isotypes: Haiti, Leg. R[ev]. P. Bertrand, Herb. J. Cardot (H); Haiti, leg. Rev. Bertrand, Herb. R. Renauld (H); Haiti leg. R[ev]. P. Bertrand com. Brotherus, Herb. J. Cardot (S); Haiti. Leg. R[ev]. P. Bertrand, 1888, Herb. J. Cardot (NY); Port-au-Prince, Haiti, Leg. Rev. R. P. Bertrand, 1888, ex Herbarium of the New York Botanical Garden (FH).

Renaudia subpilifera Williams, J. Wash. Acad. Sci. 20: 176. 1930. Protologue: Dominican Republic. Dominican Republic: Polo, Prov. de Barahona, 600–1200 meters, Feb. 26–March 12, 1922 (Abbot 1879c). Holotype: Dominican Republic. Dominican Republic: Prov. de Barahona, Loma la Haut, Polo, Altitude 600–1300 m or less, Feb. 26–Mr. 12, 1922. W. L. Abbot 1879c (NY); Isotype: Dominican Republic. Loma la Haut, Polo 600–1300 m, Feb. 26–Mr. 12, 1929 [sic]. W. L. Abbot 1879c. (FH).

Nomenclatural note. The protologue of *P. cuspidans* does not indicate when the type material was gathered, and most type specimens likewise give no collection date. There are, however, several Bertrand collections of *P. cuspidans* in FH, PC, and NY dated either 1887 or 1888. The material in PC and NY collected in 1887 is not marked as type material, while a collection in NY from Cardot's herbarium marked "sp. nov." is dated 1888. The "1888" collection is identical to the holotype.

Plants medium-sized to large, dull, light green yellow-green, reddish yellow, or golden brown, in stiff mats often with pendent strands. Primary stems yellow-red, creeping, in cross section with sclerodermis of 4–6 thick-walled cells, cortical cells firm-walled, hyaline to yellow, central strand absent; rhizoids sparse, in circular clusters abaxially to the leaf insertions, dark red, smooth to finely roughened, mostly not branched. Leaves reduced, erect to appressed, broadly triangular to broadly ovate, auriculate at base, 0.9–1.5 mm long, acuminate, hair-pointed; leaf cells linear-flexuose, thick-walled, porose, alar cells dark red, subquadrate to short-rectangular, upper margins serrulate. Secondary stems horizontal, erect or pendent, to 15 cm long, irregularly branched, arrested branch primordia numerous, in cross section with sclerodermis of 4–5 small, thick-walled, reddish orange cells, cortex cells enlarged, firm-walled, pale yellow, central strand absent; axillary hairs 3–6

cells long, reddish throughout, basal cells 1–2, short, quadrate to subquadrate, upper cells 2–3, long-cylindrical; rhizoids not seen. Secondary stem and branch apices narrowly elongate and terete; leaves ovate-deltoid to broadly ovate, not ranked, wide-spreading to erect-spreading from the base when dry, erect to erect-spreading when wet, 2–3 mm long, concave, clasping at base, auriculate, apex acuminate, long-cuspidate to hair-pointed, leaf tips straight; margins broadly incurved, entire below, serrulate below the apex; costa absent; leaf cells linear-flexuose, porose throughout, median cells $30\text{--}60 \times 4\text{--}6 \mu\text{m}$, basal cells shorter and broader, alar cells extensively developed, subquadrate to short-rectangular, $14\text{--}30 \times 10\text{--}14 \mu\text{m}$, yellow-red, reddish orange or red. Dioicous. Perigonia gemmate, lateral on secondary stems and branches, 1.0–1.3 mm long, outer perigonial leaves clasping at base, squarrose recurved above, 0.8–1.0 mm long, inner perigonial leaves broadly ovate below, long-acuminate above, orange-red across the base, cells elongate-flexuose, porose throughout, costa absent; paraphyses and curved-cylindrical antheridia numerous. Perichaetia terminal on short lateral branches, unfertilized perichaetia to 2 mm long; paraphyses and archeogonia numerous; leaves clasping below, squarrose above; fertilized perichaetia with hairy vaginula; outer leaves to 2 mm long, inner leaves oblong-lanceolate, long-acuminate, 3 mm long; costa absent, laminal cells long-linear and porose. Setae elongate, 6–8 mm long, smooth to lightly roughened below, papillose above, red to reddish yellow. Capsules exserted, erect, ovoid to short-cylindrical, 1.8–2.0 mm long; exothecial cells subquadrate to irregularly short-rectangular, firm-walled; stomata superficial on neck; opercula long-rostrate, 1.6–2.0 mm long; annuli rudimentary; peristome yellowish white, exostome to 0.5 mm long, dorsal (outer) surface lightly horizontally striate at base, finely papillose above, trabeculae weakly developed on both sides, endostome nearly as long as exostome, basal membrane low, segments filamentous, narrowly perforated, papillose, cilia rudimentary or absent. Mature calyptra not seen, immature calyptra cucullate, hairy. Spores round, lightly roughened, 18–22 μm .

Etymology. The specific epithet *cuspidans*, a Latin active present participle, means “pointed” and, refers to the long, terete stem and branch buds of the species.

Distribution. Caribbean (Cuba, Haiti, Dominican Republic).

Illustrations. Williams (1930, Fig. A 7–10); Duarte-Bello (1997, Pl. 201); Buck (1998, Pl. 90 7–12). Figures 1 & 2.

Ecology. Over limestone on road banks and on rotten logs, tree trunks, branches, and twigs, often pendent; 1158–1940 m.

Selected specimens examined. CUBA. Santiago de Cuba: *Clement* (S). HAITI. Ouest: *Imshaug 22806* (NY); Sud: *Duncan 53a* (MO); Sud-est: *Buck*

9453 (NY). DOMINICAN REPUBLIC. Barahona: Steere 22825 (H, NY); Independencia: Buck 14639 (B, NY); La Estrelleta: Buck 4573 (NY); La Vega: Norris et al. 4999 (NY); Pedernales: Steere 22907 (H, NY).

Pilotrichella cuspidans has long, terete apical buds, deltoid stem leaves, and long-cuspidate to hair-pointed leaves. Seta length is a variable feature of most *Pilotrichella* species, but those of *P. cuspidans* are consistently short, and never more than 9 mm long. Unlike most other members of the genus which have massive irregularly shaped spores, *P. cuspidans* has small (18–21 μm), more or less round spores. The presence of hair-pointed stem and branch leaves make most collections of *P. cuspidans* unmistakable. There are, however, some collections of *P. cuspidans* with cuspidate stem and branch leaves that can be difficult to separate from *P. reesei*. In these cases it is necessary to examine the shape and length of the apical buds. In *P. cuspidans* the apical buds are exceptionally long and smoothly julaceous, no other species of *Pilotrichella* has this feature.

Pilotrichella flexilis differs *P. cuspidans* in having short, swollen apical buds and broad, oblong-ovate stem leaves with short mucros that are mostly recurved. Although the alar cells in *P. cuspidans* and *P. flexilis* are similar in color, those of *P. cuspidans* are more extensively developed than those of *P. flexilis*. The plants in some collections of *P. cuspidans* are noticeably smaller than those of *P. flexilis*, but *P. cuspidans* is so variable in size that this feature can not be relied on to separate the two species. The setae in *P. cuspidans* are generally smaller than those of *P. flexilis* which typically have setae greater than 10 mm long. Both species have similar exostome ornamentation and endostome development.

There are some collections of *P. cuspidans* with relatively short leaf apices and weakly developed apical buds (see e.g., Allard 17620 NY) that are difficult to distinguish from *P. mauiensis*. The presence in *P. mauiensis* of broadly ovate leaves and fewer alar cells that are restricted to the moderately developed auriculate-angle serves to distinguish it from all collections of *P. cuspidans*.

Pilotrichella reesei can be especially difficult to distinguish from *P. cuspidans* because it has somewhat attenuate stem apical buds, distinctly auriculate leaves, and similar alar cell development. In *P. reesei*, however, the branch apical buds are short and swollen, flagelliform branches sometimes occur, and its leaves are short-cuspidate (identical to those of *P. mauiensis*) to mucronate. Furthermore, while most of the leaf apices in *P. reesei* are erect, occasionally the leaves have recurved mucros (identical to those of *P. flexilis*).

2. *Pilotrichella flexilis* (Hedw.) Ångstr., Kongl. Svenska Vetensk. Acad.

Handl. 33(11): 34. 1876. *Leskea flexilis* Sw. ex Hedw., Sp. Musc. Frond. 234. 1801. *Hypnum flexile* (Hedw.) Sw. in Brid., Muscol. Recent. 2(2): 153. 1801. *Hookeria flexilis* (Hedw.) Sm., Trans. Linn. Soc. London 9: 281. 1808. *Isothecium flexile* (Hedw.) Brid., Bryol. Univ. 2: 361. 1827. *Neckera flexilis* (Hedw.) C. Müll., Syn. Musc. Frond. 2: 129. 1850. *Meteorium flexile* (Hedw.) Mitt., J. Linn. Soc., Bot. 12: 438. 1869. *Pilotrichum flexile* (Hedw.) C. Müll. in: Par., Index Bryol. (ed. 2). 4: 4. 1905. Protologue: Jamaica. Jamaica et insulae australes [Swartz]. Holotype: *Leskea flexilis* Spec. Musc. 234. Tab. 96. *Hypnum flexile* Swartz Prod. p. 141 (G) Isotypes: *Hypnum flexile* Swz. N^o 2069, Herbarium Swartz (S); Jamaica, Swartz (H); a celeb D. D. Ol. Swartz. Jamaica (S); *Leskea flexilis* Fl. Ind. Occ. from D. Swartz, Herb. Hooker, H. 2592 (BM).

Pilotrichum cochlearifolium C. Müll., Linnaea 43: 599. 1843. *Neckera cochlearifolia* (C. Müll.) C. Müll., Syn. Musc. Frond. 2: 130. 1850. *Pilotrichella cochlearifolia* (C. Müll.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 223. 1872. *Meteorium cochlearifolium* Mitt. ex Par., Index Bryol. (ed. 2) 4: 2. 1905. Protologue: Mexico. Habitat in regno Mexicano, ubi legit Cl. C. Ehrenberg. Lectotype: Mexico: leg. C. Ehrenberg (JE, designated here). Isolectotypes: Mexico leg. C. Ehrenberg (H, S).

Neckera turgescens C. Müll., Syn. Musc. Frond. 2: 131. 1850. *Meteorium turgescens* (C. Müll.) Mitt., J. Linn. Soc., Bot. 12: 440. 1869. *Pilotrichella turgescens* (C. Müll.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 223. 1872. Protologue: Mexico. Mexico: C. Ehrenberg. Lectotype: Mexico. Ehrenberg. Müller in Hb. Hook. (BM). Isolectotypes: Mexico. Ehrenberg. Müller in Hb. Hook. (H, NY); Mexico: C. Ehrenberg (S).

Meteorium orbifolium Mitt., J. Linn. Soc., Bot. 12: 440. 1869, illegitimate name, includes an earlier name in synonymy. Based on: Mexico, Ehrenberg (H, JE, S); ins. Taboga, Seemann.

Pilotrichella recurvo-mucronata C. Müll., Bull. Herb. Boiss. 5: 563. 1897. Protologue: Guadeloupe and Puerto Rico. Guadeloupe: L'Herminier: Puerto Rico, prope Uticado, in sylva primaeva: *Sintensis* 10. III. 1889. Lectotype: Guadeloupe: L'Herminier (BM, designated here). Isolectotypes: Guadeloupe: L'Herminier (H, FH, NY, S).

Pilotrichella eroso-mucronata C. Müll., Bull. Herb. Boiss. 5: 563. 1897. Protologue: Jamaica. Jamaica, New Haven Pass, inter *Capressinam arcuatipedem*: W. Fawcett, 1896. Type not seen, synonymized by Britton (1913).

Pilotrichella squarrulosa C. Müll. in Broth., Acta Soc. Sci. Fenn. 19(5): 24. 1891. Protologue: Brazil. Prov. Minas Geraës, Caraça; sterilis [E.

Wainio]. Lectotype: Brasilia, prov. Minas Geraës, Caraça 1885. leg. *E. Wainio* (H, designated here). Isolectotypes: Brasilia, Minas Geraës, Caraça 1885 leg. *E. Wainio*, comm. Brotherus (BM, PC).

Pilotrichella pallidicaulis C. Müll., Bull. Herb. Boissier 6(2): 117. 1898. Protologue: Brazil. Brasilia, Sa. Catharina, Serra Geral, in araucarieto ad truncos arborum, Januario 1891 c.fr. parcissimis vetustis atque junioribus: *E. Ule*, Coll. 1164; Minas Geraës, Serra Italiaia, 2000 m alta, ad arbores sylvestres, Febr. 1894; sterilis: *idem*, Coll. N^o 1844. Lectotype: Brasilia, Serra do Itatiaia, an Bäumen im Walde 2000 m, 2/1894, leg. *E. Ule* 1844 (H, designated here).

Pilotrichella araucarieti C. Müll., Hedwigia 40: 85. 1901. Protologue: Brazil. Brasilia, Sa. Catharina, Serra Geral, in truncis arborum araucarieti, Januario, Martio et Majo 1890 et 1891: *E. Ule*, Coll. L, M. N^o 873, 874, 1022. Lectotype: Brasilia, prov. S. Catharina, Serra Geral, an Baumstaminen in Araucarienwalde, Maji 1890, leg. *E. Ule* 873 (H, designated here). Syntype: *E. Ule* 874 (H).

Pilotrichella araucarieti var. *crassicaulis* C. Müll., Hedwigia 40: 85. 1901, illegitimate name, includes the type of an earlier name. Based on: Brazil. In idem locis: *idem*, Coll. N^o [*Ule*] 868 (H); Minas Geraës, Serra Itabira, in truncis arborum sylvestrium, Febr. 1892: *E. Ule*, Coll. N^o 1459 sub *Pil. squarruloso* C. M. (H); Serra Caraça: *E. Wainio* (1885) in Hb. Brotheri (H); Rio de Janeiro, Mte. Tijuca, Oct. 1893: *E. Ule*, Coll. N^o 1688 (H), 1689 (H) sub *Pil. sediramea* C. M.; Petropolis, in pseudobulbis Orchidearum: Hb. Döring 1862.

Pilotrichella sediramea C. Müll., Hedwigia 40: 85. 1901. Invalid name, lacking a description and mentioned in synonymy. Based on: [Brazil] Rio de Janeiro, Mte. Tijuca, Oct. 1893: *E. Ule* Coll. N^o 1688, 1689 (both H).

Pilotrichella rigens Card., Rev. Bryol. 37: 8. 1910. Protologue: Mexico. Etat de Hidalgo: Honey-station, 1904 (*Pringle*, n. 15061). Holotype: Plantae Mexicanae. State of Hidalgo, Honey Station, 10 May 1904, *C. G. Pringle* 15061 (PC). Isotype: Plantae Mexicanae. State of Hidalgo, Near Honey Station, 10 May 1904, *C. G. Pringle* 15061 (NY).

Pilotrichella flexilis var. *robusta* Broth. In: Thér., Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 14: 360. 1940. Invalid name, lacking a description. Based on: Cuba, Sierra de Banao, Santa Clara (*Léon* 8,326) (NY).

Pilotrichella perrobusta P. de la Varde, Rev. Bryol. Lichénol. 19: 153. 1950. Protologue: Madagascar. Sommet oriental du massif de Marojéjy (N.E.) a l'ouest de la haute Manantenina, affluent de la Lokoho.

Gneiss et quartzite. Alt. 1850–2100 m. [*H. Humbert*]. Holotype: Madagascar. Sommet oriental du massif de Marojéjy (Nord-Est) a l'ouest de la haute Manantenina, affluent de la Lokoho. Gneiss et quartzite. Altitude. 1850–2137 m. Date de la récolte: 26 Mars–2 Avril 1949. Leg. *H. Humbert & G. Cours* (PC).

Pterobryopsis subcochlearifolia Thér. in Crum & Arzeni, Rev. Bryol. Lichénol. 22: 155. 1953. Invalid name, lacking a description and mentioned in synonymy. Based on: Panamá, s.l., Bro. *Hélión*, 1906 (H).

Nomenclatural note. Wijk et al. (1967) considered *P. araucarieti* an illegitimate name because its syntypes included the type of a species (*P. squarrulosa*) of earlier priority. This is not so, rather the variety *Pilotrichella araucarieti* var. *crassicaulis* is illegitimate because its protologue does included the type of *Pilotrichella squarrulosa*.

Plants medium-sized to large, dull, light green, green, yellow-green, reddish yellow, or golden brown, in loose mats, often with pendent strands. Primary stems yellow-red, creeping, in cross section with sclerodermis of 4–6 small, thick-walled cells, cortical cells enlarged, firm-walled, hyaline to yellow, central strand absent; rhizoids sparse, in circular clusters abaxially to the leaf insertions, dark red, smooth to finely roughened, mostly not branched. Paraphyllia absent. Pseudoparaphyllia absent, scale leaves present over branch buds. Leaves reduced, erect to appressed, ovate-oval, at times panduriform, 1.2–2.0 mm long, apex obtuse-rounded, mucronate to apiculate; leaf cells linear-flexuose, thick-walled, porose, alar cells subquadrate to short-rectangular. Secondary stems horizontal, erect or pendent, to 30 cm long, irregularly branched; in cross section with sclerodermis of 4–5 small, thick-walled, reddish orange cells, cortex cells enlarged, firm-walled, pale yellow, central strand absent; axillary hairs 3–5 cells long, reddish throughout, basal cells 1–2, short, quadrate to subquadrate, upper cells 2–3, long-cylindrical; rhizoids not seen. Secondary stem and branch buds short and swollen; leaves broadly oblong-ovate, not ranked, turgid, spreading to erect-spreading from the base, often with one margin broadly twisted inward when dry, erect to erect-spreading when wet, 1.7–3.0 mm long, to 1.6 mm wide, concave, clasping at base, variously auriculate; apex acute, generally mucronate, occasionally rounded or shortly apiculate, leaf tips mostly reflexed; margins broadly incurved above, often almost meeting at upper margins, entire below, usually serrulate below the apex; costa absent; leaf cells linear-flexuose, consistently porose at base, porose to occasionally smooth above, median cells 50–80 × 4–6 μm , basal cells shorter and broader, alar cells bulging in excavate groups, subquadrate to short-rectangular, 10–18 × 8–12 μm , usually dark red or reddish orange. Plants at times with

deciduous leaves on short branches. Dioicous. Perigonia gemmate, lateral on secondary stems and branches, 1.0–1.5 mm long, outer perigonial leaves clasping at base, squarrose-recurved above, 0.8–1.0 mm long, inner perigonia leaves broadly ovate, orange-red across the base, cells elongate-flexuose, porose throughout, costa absent; paraphyses and curved-cylindrical antheridia numerous. Perichaetia terminal on short lateral branches, unfertilized perichaetial to 2 mm long; paraphyses and archegonia numerous; leaves clasping below, squarrose above; fertilized perichaetia with densely hairy vaginula; leaves sheathing, outer leaves to 1.5 mm long, inner leaves oblong-lanceolate, long-acuminate, 3.5–4.0 mm long; costa absent, laminal cells long-linear and porose. Setae elongate, 3–15 mm long, smooth below and papillose above or papillose-roughened throughout, red. Capsules exserted, erect, ovoid to short-cylindrical, 1.8–2 mm long; exothecial cells subquadrate to irregularly short-rectangular, firm-walled; stomata superficial on neck; opercula long-rostrate, 1.6–2.0 mm long; annuli rudimentary; peristome yellowish white, exostome teeth 0.57 mm long, dorsal (outer) surface lightly horizontally striate at base, finely papillose above, trabeculae weakly developed on both sides, endostome nearly as long as exostome, basal membrane low, segments filamentous, narrowly perforated, papillose, cilia rudimentary or absent. Calyptrae cucullate, 3–6 mm long, densely hairy. Spores oblong, lightly roughened, 36–64 μm .

Etymology. The specific epithet *flexilis* is a Latin adjective meaning “pliant or flexible” and refers to its long, flexuose, pendent stems.

Distribution. Mexico; Central America (Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panamá); Caribbean (Cuba, Jamaica, Haiti, Dominican Republic, Puerto Rico, Guadeloupe, Dominica, Martinique); South America (Colombia, Venezuela, Ecuador, Peru, Bolivia, Brazil); Africa (Tanzania, Malagasy Republic).

Illustrations. Bartram (1949, Fig. 118 D–F); Potier de la Varde (1950, Fig. 5); Sharp et al. (1994, Fig. 536); Churchill and Linares (1995, Fig. 126 a–d); Buck (1998, Fig. 90 1–6); Duarte-Bello (1997, Pl. 202); Parra Cuspoca et al. (1999, Fig. 42); Restrepo and Para Cuspoca (2000, p. 108–109); Gradstein et al. (2001, Fig. 156 L–O). Figures 3 & 4.

Ecology. Often pendent on tree trunks and branches, shrubs, palm fronds, vines, twigs, also on stumps, rotting logs, soil of road banks, boulders, and on ground 600–3200 m (Central America); 550–2600 m (West Indies); 750–3550 m (South America); 1700–2140 m (Africa).

Selected specimens examined. MEXICO. Baja California: *Brandegee s.n.* (NY); Chiapas: *Breedlove 25849* (MO); Guerrero: *Croat 45663* (H, MEXU, MO, NY, US); Hidalgo: *Pringle, Plantae Mexicanae 10468* (FH, H, JE, L, MO, NY, S); Jalisco: *Crum 1061* (NY, US); Oaxaca: *Norris 77587*

(MO); Puebla: *Pringle 10856* (FH); Tamaulipas: *Sharp 8713* (FH); Veracruz: *Frahm 792298* (B, MO).

CENTRAL AMERICA. BELIZE. Cayo: *Allen 15238* (MO); Toledo: *Allen 18813* (BRH, MO). GUATEMALA. Alta Verapaz: *Standley 92407* (FH, NY); Chimaltenango: *Standley 58729* (FH); Chiquimula: *Steyermark 30601* (FH); El Progreso: *Steyermark 43550* (FH); Guatemala: *Standley 80694* (FH, NY); Huehuetenango: *Steyermark 48473* (FH, NY, US); Jalapa: *Steyermark 32487* (FH); Quezaltenango: *Sharp 2207* (FH, MO, US); Sactepéquez: *Standley 65103* (FH); San Marcos: *Sharp 5472* (NY); Sololá: *Steyermark 47236* (FH, MO, NY); Totonicapán: *Standley 62651* (FH). EL SALVADOR. Ahuachapán: *Monro et al. 2051* (MO); Santa Ana: *Davidse et al. 37193* (MO). HONDURAS. Atlántida: *Allen 17364* (MO, TEFH); Comayagua: *Allen 13999* (MO, TEFH); Cortés: *Allen 14221* (MO, TEFH); El Paraíso: *Nelson 4799* (MO); Francisco Morazán: *Allen 12366* (MO, NY, TEFH); Lempira: *Allen 11273* (MO, TEFH); Ocotepeque: *Allen 14446* (MO, TEFH); Olancho: *Allen 12699* (MO, TEFH). NICARAGUA. Estelí: *Stevens 16296* (MO, NIC, NY); Granada: *Almedo 1459a* (CINN, MO); Jinotega: *Henrich & Stevens 421* (MO, NIC, NY); Matagalpa: *Davidse et al. 30505* (MO, S); Rivas: *Stevens 6543* (MO). COSTA RICA. Alajuela: *Croat 43482* (MO); Cartago: *King C91-80* (MO); Heredia: *Crosby 3879* (MO); Limón: *Davidse et al. 25797* (CR, MO); Puntarenas: *Lyon 147* (MO); San José: *Cryptogamae exsiccatae 3599* (B, BM, H, L, MO, NY, S, US). PANAMA. Bocas Del Toro: *Allen 5236* (H, MO); Chiriquí: *Allen 5346* (MO); Colón: *Croat 33642B* (MO); Darién: *Allen 8896* (MO).

CARIBBEAN. CUBA. Granma: *Pócs & Duany 9083A* (MO, NY); Holguín: *Acuna & Morton 3916* (NY); Sancti Spíritus: *Clément & León 6544* (NY); Santiago de Cuba: *Buck 7738* (NY); Villa Clara: *Pócs & Borhidi 9011/V* (MO). JAMAICA. Portland: *Crosby 3164* (MO); St. Andrew: *Grout, North American Musci Pleurocarpi 389* (H, FH, MO, NY, S, US); St Thomas: *Hegewald & Hegewald 8146* (MO). HAITI. Sud: *Ekman 606* (NY, S). DOMINICAN REPUBLIC. Peravia: *Steere 23177* (NY); Puerto Plata: *Reese 15446* (NY); La Vega: *Norris 5724* (H, MO, NY). PUERTO RICO. Aguadilla: *Steere 5602* (FH, MO, NY); Guayama: *Steere 4627* (FH, MO, NY); Humacao: *Steere 4018* (MO); Mayagüez: *Steere 5514* (FH, MO, NY); Ponce: *Steere 6178* (FH, MO). GUADELOUPE. *L'Herminier s.n.* (FH, NY). DOMINICA. *Elliott 669b* (FH). MARTINIQUE. *Webster 734* (BM).

SOUTH AMERICA. VENEZUELA. Aragua: *Pursell et al. 9290* (MO); Barinas: *Dorr et al. 4872* (MO, NY); Bolívar: *Steyermark & Wurdack 844* (B, FH, MO, NY); Carabobo: *Steyermark & Steyermark 95564* (MO); Distrito Federal: *Steyermark et al. 127874* (MO); Falcon: *Griffin & Wingfield PV-1646* (MO); Lara: *Meijer et al. 124* (B, G, H, MO, NY, S, US, VEN); Mérida:

Griffin et al. 017476 (H, JE, MO, NY); Monagas: *Steyermark 62111b* (FH); Portuguesa: *Steyermark et al. 126620* (MO); Táchira: *Davidse & González 22105* (MO); Trujillo: *Liesner et al. 13031* (MO). COLOMBIA. Antioquia: *MacDougal et al. 4446* (MO, NY); Boyacá: *Churchill et al. 19011* (COL, MO, NY); Cauca: *Barclay & Juajibioy 6022-A* (MO); Chocó: *Churchill et al. 14536* (NY); Magdalena: *Mägdefrau 1066* (B); Narino: *Ramírez 10929* (MO); Norte de Santander: *Steere 7307* (NY); Putumayo: *Ramírez 10286* (MO); Santander: *Lewis 88-1307* (B, MO, NY); Valle: *Churchill et al. 15342* (CUVC, MO, NY). ECUADOR. Carchi: *Steere 9098* (NY); Imbabura: *Solís 8264* (NY); Loja: *Holm-Nielsen et al. 3679* (MO, S); Morona-Santiago: *Steere 27799* (NY); Napo: *Steere 9139* (NY); Pastaza: *Steere 8425* (NY); Pichincha: *Steere & Balslev 25566* (H, NY); Zamora: *Steere & Balslev 25826* (NY). PERU. Cajamarca: *Campos et al. 5252* (MO); San Martin: *Smith C295* (MO). BOLIVIA. Cochabamba: *Price et al. 1476* (MO); La Paz: *Lewis 89-990* (MO); Santa Cruz: *Nee 40677* (MO, NY, S). BRAZIL. Bahia: *Harley et al. 26238* (NY); Minas Geraes: *Vital & Buck 11535* (NY); Paraná: *Bauer, Musci Europ. et Amer. 2248* (BM, FH, H, L, MO, NY, S); Rio de Janeiro: *Landrum 2181* (MO, NY); Rio Grande do Sul: *Wasum et al. 4248* (MO); Santa Catarina: *Vital & Buck 12382* (NY); Sao Paulo: *Schäfer-Verwimp 6954* (MO).

AFRICA. TANZANIA. Kilosa: *Inoue, Bryophyta Selecta Exsiccata 735* (H, JE, MO, NY, S); Morogoro: *Pócs 6467/D* (MO, NY). MALAGASY REPUBLIC. Antananarivo: *Pool s.n.* (NY). Antseranana: *Crosby & Crosby 7149* (BM, G, FH, H, MO, NY, US).

Pilotrichella flexilis is the most widespread species in the genus, there are thousands of herbarium collections of it. It is frequently encountered growing in dense pendent masses in shaded, very humid places. The species is remarkably stenotypic in most of its features and can often be recognized with a hand-lens by its usually golden-reddish color, turgid appearance, and erect-spreading leaves that are somewhat twisted above when dry and have consistently recurved mucros. Not all leaves in a single collection are liable to have recurved mucros, but the feature can always be found on at least some (usually most) leaves. The leaves near the branch buds are especially likely to have recurved mucros.

The leaves of *P. flexilis* are absolutely ecostate and consistently have auriculate leaf bases with bulging-excavate, generally dark-red alar cells, linear-flexuose, strongly porose cells, and broadly incurved upper margins. There are some collections of *P. flexilis* with straight-walled or very weakly porose upper leaf cells. These collections also are consistently green to light-green in color, and this suggests the feature may be associated with even

more shaded, humid habitats than is normal for the species. The feature does not appear to be of taxonomic value since there are collections that exhibit all gradations of straight-walled to strongly porose upper leaf cells.

The leaves of *P. flexilis* are characteristically mucronate, but mucro length varies considerably within the species. Plants at one end of the variation have most leaves with rounded apices; leaves with distinct mucros occur only sporadically. This extreme is geographically centered in African and nomenclaturally centered on *P. perrobusta*.

Plants from Central and South America, however, occasionally have this type of leaf variation. The opposite extreme occurs in the Caribbean (see i.e., Cuba, Pócs & Borhidi 9011/W MO) where some plants with long mucronate leaves closely approach the leaves of *P. cuspidans* and *P. mauiensis*. This Caribbean expression of *P. flexilis* differs from *P. cuspidans* and *P. mauiensis* in having distinctly recurved leaf mucros.

Pilotrichella flexilis has exserted, shortly cylindrical capsules on setae that are usually 10 mm long. Its setae, however, vary from 3 mm long to 15 mm long. This variation in seta length does not appear to have taxonomic value since some collections have single stems with setae that range 3 mm to 11 mm long.

The upper leaf margins directly below the apex in *P. flexilis* are serrulate as the result of projecting cell ends. There seems to be a direct correlation between the degree of upper leaf margin incurving and marginal serrulation. Leaves with the strongest incurved margins have the most distinct marginal serrulations. Some collections of *P. flexilis* have leaves with entire margins, but even these collections also have some leaves with weakly serrulate upper leaf margins.

Pilotrichella flexilis has been confused with *Squamidium nigricans* (Hook.) Broth. and *Phyllogonium viscosum* (P. Beauv.) Mitt. These species are similar to *P. flexilis* in overall aspect, they grow in pendent masses, and their leaves have recurved mucros. *Squamidium nigricans* is a smaller plant than *P. flexilis*, it has spirally ranked leaves, and often the plants have an intense blackish color. It also differs from *P. flexilis* in having immersed capsules, and leaves with long (but faint) single costae. The alar cells in *S. nigricans* are more extensively developed than those of *P. flexilis*, they are often hyaline rather than reddish yellow, and not as strongly bulging as the alar cells of *P. flexilis*. *Phyllogonium viscosum* and *P. flexilis* have auriculate leaves and linear-flexuose, strongly porose leaf cells. The genus *Phyllogonium* is characterized by its distichous, conduplicate leaves and this feature usually can be relied on to separate it from *P. flexilis*. *Phyllogonium viscosum* however has swollen, turgid leaves that tend to obscure the distichous nature of the leaves. The costa in *P. viscosum* varies from

short-double to absent, and this feature can be used to distinguish it from *P. flexilis* which is absolutely ecostate.

There is a collection of *P. flexilis* at the Missouri Botanical Garden labelled "Bermuda" The specimen is a duplicate from the "Elizabeth Gertrude Britton Moss Herbarium" at the New York Botanical Garden. There is no duplicate of this specimen at NY. It is very unlikely this specimen came from Bermuda which lacks the habitats and elevation commonly associated with *P. flexilis*. It seems more plausible that this is a labeling error.

2a. *Pilotrichella flexilis* form *nudiramulosa* (C. Müll.) Allen & Magill, *forma nova*.

Pilotrichella nudiramulosa C. Müll., Hedwigia 40: 85. 1901. Protologue: Brazil. Brasilia, Sa Catharina, Serra Geral, ad truncos Araucariae Brasiliensis: E. Ule, Junio 1890, Coll. N^o 867. Lectotype: Brasilia, prov. S. Catharina, Serra Geral, an Stammen von Araucaria, Junii 1890. leg. E. Ule 867 (H).

Etymology. The epithet *nudiramulosa* combines the Latin adjectives *nudus* "naked" and *ramulosus* "bearing branchlets" in reference to its short branches with deciduous leaves.

Distribution. Mexico; Central America (Costa Rica, Panamá); South America (Colombia, Ecuador, Peru, Brazil); Africa (Madagascar).

Illustration. Figure 2 F.

Ecology. On tree trunks and branches; 800–2700 m.

Selected specimens examined. MEXICO. Chiapas: *Breedlove* 14403 (MO); Hidalgo: *Vela* 598 (US); Veracruz: *Arséné* 8003 (FH).

COSTA RICA. Alajuela: *Brenes* 16691 (FH, NY); Cartago: *Standley* 33582 (FH, US); Heredia: *Tonduz s.n.* [Pl. Costaricensis N^o 5680] (G); Puntarenas: *Haber* 6211 (CR, MO, NY); San José: *Crosby* 10882 (CR, MO). PANAMA. Chiriquí: *Croat* 13746 (MO).

COLOMBIA. Cundinamarca: *Apollinaire s.n.* (G). ECUADOR. Loja: Loja: *André* K1801 [8 Nov.] (NY); Pichincha: *Spruce* 1232 (BM). PERU. Arequipa: *André* K1801 [17 Nov. 1876] (FH); BRAZIL. Rio Grande do Sul: *Lindman* 122 (BM, H, S); Santa Catarina: *Ule* 169 (B, BM, FH, JE, L, NY, S); Sao Paulo: *Wacket* 1235 (H).

MALAGASY REPUBLIC. Antseranana: *Magill et al.* 9948 (MO).

Pilotrichella flexilis form *nudiramulosa* is generally a smaller plant than most collections of *P. flexilis*. Typically it has short branches with leaves so deciduous that the branches are often naked. Plants of *P. flexilis* form *nudiramulosa* exhibit considerable gametophytic variation throughout their range, especially in the development of deciduous leaves. Gametophytic variation in form *nudiramulosa* shows more or less discrete geographical pat-

terns, and this may indicate the taxon is not monophyletic. Rather the multiple evolution of this form may have been driven by the fact that deciduous leaves in a species rarely producing sporophytes would significantly increase the ability of the plants to spread asexually.

Pilotrichella mauiensis is similar in size to form *nudiramulosa*, and sometimes it also has short branches with deciduous leaves. The presence of flagelliform branch tips in *P. mauiensis* as well as slender branchlets with microphyllous leaves will often distinguish it from *P. flexilis* form *nudiramulosa*. Furthermore, the leaves of *P. mauiensis* are not nearly as auriculate at base as those of *P. flexilis*, and its usually cuspidate leaf apices are erect rather than recurved.

The ranges of *P. flexilis* form *nudiramulosa* and *P. mauiensis* overlap in Central America and Mexico. Unfortunately, collections of form *nudiramulosa* in these regions have inconsistently recurved leaf mucros. These collections are exceedingly difficult to distinguish from collections of *P. mauiensis* that have short cuspidate leaves. When slender branchlets and flagelliform branch tips are also absent from the collections of *P. mauiensis* with short cuspidate leaves the two taxa are essentially indistinguishable.

3. *Pilotrichella mascarenica* (C. Müll.) Jaeg., Ber. Thätigk. St. Galischen Naturwiss. Ges. 1875–76: 259. 1877. *Neckera mascarenica* C. Müll., Bot. Zeitung (Berlin) 17: 237. 1859. Protologue: Réunion. Insula Borboniae: Bory de St. Vincent. Lectotype: Isle de Bourbon, Bory St. Vincent (G). Isolectotypes: Isle de Bourbon, Bory St. Vincent (BM); Bourbon, Bory (L); Mascareignes, Bory de St. Vincent (H).

Pilotrichella isleana Besch., Ann. Soc. Nat., Bot. sér. 6, 10: 267. 1880. Protologue: Réunion. La Réunion: plaine des Cafres, associé au *Phyllogonium*, G. de L = Isle, 1875. Holotype: La Reunion. Plaine de Cafres, G. de Isle (BM).

Pilotrichella islei Besch. ex Kindb., Enum. Bryin. Exot., Suppl. 2. 102. 1891, orthographical variant of *P. isleana* Besch.

Pilotrichella hampeana Kiaer. In: Wright, J. Bot. 26: 266. 1888, invalid name, lacks a description. Based on: Madagascar, Mt. Ankaratra (*Borgen 30*). Musci Madagascarienses, Herb. Kiaer. In montibus Ankaratra 1877–1879 legit M. Borgen N^o 30 (H); Musci Madagascarienses, Herb. Kiaer. In montibus Ankaratra 1875 legit M. Borgen N^o 30 (L).

Nomenclatural note. The two specimens on which the name *Pilotrichella hampeana* is based bear identical printed labels. The label on the specimen from L, however, has the date 1879 inked out and the date 1877 changed to 1875.

Plants small to medium-sized, dull, light green, green, yellow-green, or golden brown, in loose mats often with pendent strands. Primary stems red, creeping, in cross section sclerodermis with 4–5 small thick-walled cells, cortical cells enlarged, firm-walled, hyaline to yellow, central strand absent; rhizoids sparse, in circular clusters abaxially to the leaf insertions, dark red, smooth, mostly not branched. Paraphyllia absent. Pseudoparaphyllia absent, scale leaves present over branch buds. Leaves reduced, erect to appressed, ovate-oval, at times panduriform, to 1.4 mm long, apex obtuse-rounded, mucronate to apiculate; leaf cells linear-flexuose, thick-walled, porose, alar cells subquadrate to short-rectangular. Secondary stems arising irregularly from the primary stems, often pendent, to 14 cm long, irregularly branched, in cross section sclerodermis with 4–5 small, thick-walled, reddish orange cells, cortex cells enlarged, firm-walled, pale yellow, central strand absent; axillary hairs, 3–4 cells long, basal cells 1–2, short, quadrate to subquadrate, reddish, upper cells 2, long-cylindrical, yellowish; rhizoids rare, at base of branches, dark red, smooth, mostly not branched. Secondary stem and branch buds short and swollen; leaves oblong-ovate, not ranked, turgid, erect to erect-spreading from the base when dry, erect-spreading when wet, 1.2–1.6 mm long, concave, clasping at base, variously auriculate; apices acute, mucronate to shortly apiculate, leaf tips often reflexed; margins broadly incurved above, usually meeting or overlapping at upper margins, entire below, usually serrulate below the apex; costa absent; leaf cells linear-flexuose, porose, median cells $30\text{--}60 \times 3\text{--}4 \mu\text{m}$; basal cells shorter and broader, alar cells bulging in excavate groups, subquadrate to short-rectangular, $10\text{--}28 \times 10\text{--}20 \mu\text{m}$, usually dark red or reddish orange. Dioicous. Perigonia gemmate, lateral on secondary stems and branches, 1.0 mm long, outer perigonial leaves clasping at base, erect to recurved above, 0.8–1.0 mm long, inner perigonia leaves broadly ovate, orange-red across the base, cells elongate-flexuose, porose throughout, costa absent; paraphyses and curved-cylindrical antheridia numerous. Perichaetia terminal on short lateral branches, unfertilized perichaetial to 2 mm long; paraphyses and archegonia numerous; leaves clasping below, squarrose above; fertilized perichaetia with densely hairy vaginula; leaves sheathing, outer leaves to 1.5 mm long, inner leaves oblong-lanceolate, long-acuminate, 3.5–4.0 mm long; costa absent, laminal cells long-linear, porose. Setae elongate, 7–8 mm long, smooth below and papillose above, red or reddish brown. Capsules exserted, erect, ovoid to short-cylindrical, 1.5–2 mm long; exothecial cells subquadrate to shortly and irregularly rectangular, firm-walled; stomata superficial on neck; opercula long-rostrate, 1.5 mm long; annuli rudimentary; peristome yellowish white, exostome teeth 0.42 mm long, dorsal (outer) surface lightly horizontally striate at base, finely papillose above, trabeculae weakly developed

on both sides, endostome 2/3 the exostome length, basal membrane low, segments filamentous, narrowly perforated, papillose, cilia rudimentary or absent. Calyptrae cucullate, 3–4 mm long, densely hairy. Spores oblong, spherical, rounded-triangular, lightly roughened, 34–54 μm .

Etymology. The specific epithet *mascarenica* refers to the Mascarene island group (Réunion, Mauritius, Rodrigues).

Distribution. Africa (Malagasy Republic, Réunion).

Illustration. Figure 5.

Ecology. On tree bark and twigs, often pendent from trees; 1350–2200 m.

Specimens examined. AFRICA. MALAGASY REPUBLIC. Antananarivo: Crosby & Crosby 5272 (MO), 5383 (MO), Cremers 1763 (MO), Camboué (H, S), Borgen 30 (H, L), Villaume (FH); Antseranana: Dufournet (S); Fianarantsoa: Crosby & Crosby 6830 (MO); Mahajanga: Humbert & Capuron s.n. (S), 29/11 1901, indigenous collector (L). REUNION. Arrondissement au Vent: Bory St. Vincent (BM, G, H, L), Een 350 (MO, S), 321 (S); Arrondissement su le Vent: Chauvet, 1894, (FH, S), Crosby & Crosby 9006 (FH, G, H, L, MO, NY, PC, S, US).

Pilotrichella mascarenica is a small to medium sized species with oblong-ovate leaves that have inconsistently recurved apices. It is identical in size to some forms of *P. mauiensis*, but that species differs from *P. mascarenica* in having cuspidate leaves with erect apices. Many collections of *P. mauiensis* also differ from *P. mascarenica* in having short branches with deciduous leaves, flagelliform branch tips or slender branchlets with microphyllous leaves. *Pilotrichella mascarenica* is identical to *P. flexilis* in many features, and both species have enlarged, irregularly shaped spores. The leaves of *P. mascarenica*, however, have strongly incurved upper leaf margins that commonly overlap just below the apex. It further differs from *P. flexilis* in having shorter, narrower leaves, and shorter setae.

Pilotrichella mascarenica is the same size as most species of *Orthostichella*. Typically *Orthostichella* has spirally arranged (especially branch) leaves, and this feature usually distinguishes it from *P. mascarenica*. There are some collections of *Orthostichella* with leaves indistinctly spirally ranked and these can be difficult to distinguish from *P. mascarenica*. The alar cells in all species of *Orthostichella*, however, are weakly differentiated and because they are not excavate-bulging the individual cells can be clearly seen.

4. *Pilotrichella mauiensis* (Sull.) Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 255. 1877. *Meteorium mauiensis* Sull., Proc. Amer. Acad. Arts 3: 182. 1855. Protologue: Hawaii. East Maui, Sandwich Islands;

on the north bank of the Crater, at an elevation of 10,200 feet. Holotype: East Maui, Sandwich Islands; on the north bank of the crater Haleakala, U.S.E.E. Wilkes 1838/42 (FH). Isotypes: East Maui, north Bauky [sic] Crater, 10200 ft high! Sandwich Island, Herbarium of the U. S. Exploring Expedition under the Command of Capt. Wilkes (NY); East Maui, Wilkes Expl. Exp. (NY); East Maui, North Bank of Crater, 10200 ft alt. Sandwich Isds. U. S. Ex. (NY); Hawaii, Wilkes Exped. E. Maui (FH).

Pilotrichella flagellifera Besch., Mexic. Pl. 39. 1872, illegitimate name, protologue includes an earlier name in synonymy. Based on: Mejico (*Ehrenberg*); Orizaba (*Bourgeau*). Mexico, Orizaba, 1866: *Bourgeau*, Herb. Émil Bescherelle: 1900. (BM). Mexico. leg. *C. Ehrenberg* (BM); Mexico. *C. Ehrenberg* (BM); Mexico, Orizaba, Herb. Hampe 1881 (BM).

Pilotrichella cochlearifolia var. *flagellifera* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 223. 1872. Protologue: Mexico. Orizaba (*Bourgeau*). Holotype. Mexico, Orizaba, 1866: *Bourgeau*, Herb. Émil Bescherelle: 1900. (BM).

Meteorium vulcanicum Mitt. In: Seem., Fl. Vit. 395. 1873. Protologue: Hawaii. Hawaii ad montem ignivomen (Macrae! in Herb. Musaei Brit.). Isotype. Owyhee. ad m. ignivomen. Macrae, Jan. 1825, sin. coll. (FH).

Pilotrichella desmoclada C. Müll., Flora 82: 464. 1896. *Weymouthia desmoclada* (C. Müll.) Broth., Nat. Pflanzenfam. 1(3): 812. 1906. Protologue: Hawaii. Insulae Hawaiicae, sine loco speciali, sed vero-similiter e regionibus altioribus: Dr. Hillebrand. Lectotype: Hawaii: sine loco designato. leg. Dr. Hillebrand (H, designated here). Isotypes: Hawaii: sine loc spec., leg. Dr. W. Hillebrand (FH); Hawaii. leg. Hillebrand (H).

Nomenclatural note. There is some confusion surrounding the type material of *P. cochlearifolium* and *P. flagellifera*. This is because the protologues of *P. cochlearifolium* and *P. flagellifera* cite similar specimens AHabitat in regno Mexicano, ubi legit Cl. C. Ehrenberg [*P. cochlearifolium*] or Mejico (*Ehrenberg*) [*P. flagellifera*], and all available type material give only "Mexico leg. C. Ehrenberg" or "Mexico. C. Ehrenberg" on their labels. This group of specimens represents two species; the material in BM is *P. flagellifera* (= *P. mauiensis*), and the material in H, JE, S is *P. cochlearifolia* (= *P. flexilis*).

Plants medium-sized, dull, light green, yellow-green, or golden brown, in stiff mats, sometimes with pendent strands. Primary stems yellow-red to red, creeping, in cross section sclerodermis with 4–6 thick-walled cells, cortical cells enlarged, firm-walled, hyaline to yellow, central strand absent; rhizoids in circular clusters abaxially to the leaf insertions, dark-red, smo-

oth to finely roughened, mostly not branched. Paraphyllia absent. Pseudo-paraphyllia absent, scale leaves present over branch buds. Leaves reduced, erect-clasping, broadly ovate, auriculate at base, 0.8–1.0 mm long; apices acuminate, hair-pointed; leaf cells linear-flexuose, thick-walled, porose, alar cells dark red, subquadrate to short-rectangular, upper margins serrulate. Secondary stems arising irregularly from the primary stems, creeping or pendent, to 25 cm long, irregularly branched; in cross section sclerodermis with 4–5 small, thick-walled, reddish orange cells, cortex cells enlarged, firm-walled, pale yellow, central strand absent; axillary hairs 4–5 cells long, basal cells 1–2, short, quadrate to subquadrate, reddish, upper cells 2–3, long-cylindrical, reddish; rhizoids present. Secondary stem and branch apices short and swollen; leaves ovate to oblong-ovate, not ranked, wide-spreading to erect-spreading, margins incurved when dry, erect-spreading when wet, 1–2 mm long, concave, clasping at base, rounded to the insertion or weakly auriculate; apex acuminate, long or short cuspidate, leaf tips straight not reflexed; margins broadly incurved above, entire below, serrulate below the apex; costa absent; leaf cells linear-flexuose, porose throughout, median cells $16\text{--}50 \times 3\text{--}4 \mu\text{m}$; basal cells shorter and broader, alar cells in bulging, excavate groups, subquadrate to short-rectangular, $14\text{--}20 \times 2\text{--}12 \mu\text{m}$, yellow-red, reddish orange or red. Plants often having slender branches with microphyllous leaves, flagelliform branch tips, or deciduous leaves. Dioicous. Perigonia gemmate, lateral on secondary stems and branches, 1.0–1.3 mm long, outer perigonial leaves clasping at base, squarrose recurved above, 0.8–1.0 mm long, inner perigonia leaves broadly ovate below, long-acuminate above, orange-red across the base, cells elongate-flexuose, porose throughout, costa absent; paraphyses and curved-cylindrical antheridia numerous. Perichaetia terminal on short lateral branches, unfertilized perichaetia to 2.5 mm long; paraphyses and archegonia numerous; leaves clasping below, squarrose above; fertilized perichaetia with hairy vaginula; leaves sheathing, outer leaves to 2.0 mm long, inner leaves oblong-lanceolate, long-acuminate, 3 mm long; costa absent, laminal cells linear and porose. Setae elongate, 5–15 mm long, smooth to lightly roughened below, papillose above, red. Capsules exserted, erect, ovoid to short-cylindrical, 1.5–2.0 mm long; exothecial cells subquadrate to short, irregularly rectangular, firm-walled; stomata superficial on neck; opercula long-rostrate, 1.0–1.5 mm long; annuli rudimentary; peristome yellowish white, exostome to 0.5 mm long, dorsal (outer) surface lightly horizontally striate at base, finely papillose above, trabeculae weakly developed on both sides, endostome $2/3$ the exostome length, basal membrane low, segments filamentous, narrowly perforated, papillose, cilia rudimentary or absent. Calyptrae cucullate, hairy, to 3.5 mm long. Spores round, irregularly rounded to oblong, lightly roughened, $20\text{--}28 \mu\text{m}$.

Etymology. The specific epithet *mauiensis* refers to the Hawaiian island on which the type of the species was collected.

Distribution. Hawaii; Mexico; Caribbean (Cuba); Central America (Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panamá); South America (Bolivia).

Illustrations. Bartram (1933, Fig. 125). Figures 6 & 7.

Ecology. On tree trunks, pendent from branches, on shrubs, vines or twigs; 120–3109 m.

Selected specimens examined. HAWAII. Hawaii: Skottsberg 1341 (FH, H, S); Kauai: Small, *Mosses of the Hawaiian Islands* 10 (F, FH, L, MO, NY, S); Maui: Hoe, *Bryophyta Hawaiica Exsiccata* 37 (B, FH, H, MO, NY, S); Oahu: Forbes, 2/12–19/09 (FH, L).

MEXICO. Chiapas: Hermann 26405 (H, MO, NY); Guerrero: Croat 45624A (FH, G, H, MO, NY, US); Hidalgo: Pringle, *Plantae Mexicanae* 10417 (B, BM, FH, G, H, JE, L, MO, NY, S); Jalisco: Crum 892 (S); Oaxaca: Maldonado & Martin 237 (MO); Puebla: Cárdenas 89 (H); San Luis Potosí: Ferguson 7 (NY); Tamaulipas: Pursell 5631 (MO); Veracruz: Hermann 28836 (NY).

CUBA. Santiago de Cuba: Clément 309 (NY).

BELIZE. Toledo: Allen 18831 (BRH, MO). GUATEMALA. Alta Verapaz: Standley 90725 (FH); Zacapa: Steyermark 43227 (FH). HONDURAS. Atlántida: Allen 17399A (MO); Lempira: Allen 11596 (MO); Yoro: Allen 13589 (MO). NICARAGUA. Estelí: Stevens & Grijalva 15632 (MO, NIC); Jinotega: Henrich & Stevens 283 (MO); Matagalpa: Granow de la Cerda 2167 (MO, NY). COSTA RICA. Alajuela: Brenes 16985 (NY); Cartago: Standley 41487 (FH, JE, S, US); Guanacaste: Dodge et al. 7915 (FH); Heredia: Crosby 10870 (H, NY); Puntarenas: Croat 47131 (MO); San José: Stevens 13704 (MO). PANAMA. Chiriquí: Croat 16057 (MO, S).

BOLIVIA. Santa Cruz: Herzog 3991 (JE).

Pilotrichella mauiensis was described from the Hawaiian islands and the species exhibits considerable variation there in plant size and overall aspect. Bartram (1933), however, considered the leaf characters of the species so consistent that he included all of its forms in a single species. The Hawaiian collections of *P. mauiensis* are instructive in showing important variations not only in plant size and aspect, but in leaf cuspid length, as well as the presence/absence of both flagelliform branch/stem apices and slender branchlets with microphyllous leaves. The plant variations exhibited by the Hawaiian plants, however, do not demonstrate the full range of variation found in the species. For example, plants of *P. mauiensis* from southern Mexico, Guatemala, Belize, and northern Honduras can be especially large

and have long-cuspidate leaves (see e.g., Hermann 28836 NY or Allen 17364 MO). When first encountered this extreme Neotropical expression seems to be distinct from the Hawaiian *P. mawiensis*. The species, however, when taken as a whole shows complete intergradation in size and leaf cuspid length. Furthermore, leaf cuspid length is remarkably variable within single collections. Critical features that separate *P. mawiensis* from other members of *Pilotrichella* include its erect, usually cuspidate leaf apices, weakly auriculate leaf bases, alar cells differentiated in a relatively small, discrete area, the occurrence of flagelliform branch apices, and the presence of slender branchlets with microphyllous leaves.

Although the slender branchlets in this species appear to be axillary, they in fact arise on the dorsal side of the leaf from the line of alar cells that marks the transition from the alar region to the laminal cells. Since they originate from a single cell they are extremely deciduous. When young the branchlets have the same appearance as the axillary propagula found in *Pohlia* Hedw., and as they begin to elongate they look similar to the axillary brood branches of *Pseudotaxiphyllum elegans* (Brid.) Iwats. When fully formed they can be 15 mm long and have microphyllous leaves with axillary brood bodies. These branchlets also occur around branch primordia. Newton (2002) gives an excellent, detailed account of these branchlets. Newton (2002) attributes these structure to *P. flexilis*, but flagelliform branchlets are unknown in that species and her plants almost certainly are *P. mawiensis*.

The leaf apices of *P. reesei* and *P. mawiensis* are similar, and both species have short, swollen apical buds as well as slender branchlets. *Pilotrichella reesei*, however, never has flagelliform branch apices, and its leaves are distinctly auriculate with extensively developed alar cells. Furthermore, the leaves of *P. reesei* differ from those of *P. mawiensis* in occasionally having shortly mucronate, recurved apices.

The leaves of *P. flexilis* and *P. mawiensis* are similar in the form and distribution of their alar cells, and both species can have deciduous leaves. Plants of *P. flexilis* are generally larger than those of *P. mawiensis*, and their leaf apices are more consistently mucronate with most of the apices distinctly recurved. *Pilotrichella flexilis* also never has flagelliform branch apices or slender branchlets.

5. *Pilotrichella reesei* Allen & Magill, *sp. nov.*

TYPE: Dominican Republic. Prov. La Vega: 12 km S of Constanza on road to Valle Nuevo, 6000 feet, 18°52'N, 70°42'W, 9 January 1987, William R. Buck 14015 (holotype NY).

Species haec a *P. cuspidanti foliis* breviter cuspidatis vel mucronatis differt.

Plants slender to medium-sized, dull, light green, yellow-green, reddish yellow, or golden brown, in loose or stiff mats, at times with pendent strands. Primary stems yellow-red, creeping, in cross section sclerodermis with 4–6 cells thick-walled cells, cortex cells enlarged, thick-walled, hyaline to yellow, central strand absent; rhizoids sparse, in circular clusters abaxially to the leaf insertions, dark-red, smooth to finely roughened, mostly not branched. Paraphyllia absent. Pseudoparaphyllia absent, scale leaves present over branch buds. Leaves reduced, erect to appressed, broadly ovate, auriculate at base, 0.9–1.5 mm long, acuminate, hair-pointed; cells linear-flexuose, thick-walled, porose, alar cells dark red, subquadrate to short-rectangular, upper margins serrulate. Secondary stems arising irregularly from the primary stems, often pendent, to 10 cm long, irregularly branched; in cross section sclerodermis with 4–5 small, thick-walled reddish orange cells, cortex cells enlarged, firm-walled, pale yellow, central strand absent; axillary hairs reddish throughout, 3–5 cells long, basal cells 1–2, short, quadrate to subquadrate, upper cells 2–3, long-cylindrical; rhizoids not seen. Secondary stem and branch apices somewhat elongate and terete to short and swollen; leaves ovate-deltoid to broadly ovate, not ranked, wide-spreading to erect-spreading from the base, margins incurved dry, erect to erect-spreading when wet, 1.7–2.5 mm long, concave, clasping at base, auriculate; apices mucronate to short cuspidate, leaf tips straight or reflexed; margins broadly incurved, entire below, serrulate below the apex; costa absent; leaf cells linear-flexuose, porose throughout, median cells $40\text{--}60 \times 3\text{--}5 \mu\text{m}$; basal cells shorter and broader, alar cells bulging in strongly differentiated, excavate groups, subquadrate to short-rectangular, $14\text{--}30 \times 10\text{--}14 \mu\text{m}$, yellow-red, reddish orange or red. Dioicous. Perichaetia terminal on short lateral branches, unfertilized perichaetia to 1.5 mm long; paraphyses and archegonia numerous; leaves clasping below, squarrose above, costa absent, cells linear and porose. Perigonia and sporophytes not seen.

Etymology. This species is named for the American bryologist and Calymperaceae specialist William Dean Reese (10 September 1928–4 February 2002).

Distribution. Mexico and the Caribbean (Cuba, Dominican Republic, Puerto Rico).

Illustration. Figure 8.

Ecology. On tree trunks, old fern fronds, and logs; 1000–1829 m.

Selected specimens examined. MEXICO. Chiapas: *Hale & Soderstrom* 20251 (MO).

CUBA. Sancti Spíritus: *Pócs & Borhidi* 3. X. 1978 (NY); Santiago de Cuba: *Buck* 7733 (NY). DOMINICAN REPUBLIC. Barahona: *Zanoni et al.* 30212 (MO); La Estrelleta: *Reese* 15340 (NY); La Vega: *Buck* 7959

(NY); Peravia: *Steere* 22838 (NY). PUERTO RICO. Ponce: *Laubengayer s.n.* (MO, NY).

Pilotrichella reesei does not appear to have a single unique feature, rather its distinctiveness resides in the presence of a unique combination of features found variously in *P. cuspidans*, *P. mauiensis*, and *P. flexilis*. The species has been confused with *P. flexilis* and *P. cuspidans*, e.g., some collections of *P. reesei* originally named *P. cuspidans* were later annotated as *P. flexilis*, and others originally named *P. flexilis* were annotated *P. cuspidans*.

Plants of *P. reesei* usually have attenuate stem apical buds, and leaves that are distinctly auriculate. These two features are indicative of *P. cuspidans*. In addition, the leaves of *P. reesei* have the extensive alar cell development characteristically found in *P. cuspidans*. These same collections, however, usually have short, swollen branch apical buds, and occasionally collections have flagelliform branchlets. These latter two features are associated with *P. flexilis* and *P. mauiensis*. The leaves of *P. reesei* are never as long-pointed as those of *P. cuspidans*, rather they vary from short cuspidate (identical to those of *P. mauiensis*) to mucronate (identical to those of *P. flexilis*). Significantly adding to the confusion surrounding this species is the fact that while usually the leaf apices are erect (a feature of *P. cuspidans* and *P. mauiensis*), occasionally its short mucronate leaves have

distinctly recurved apices (a critical feature of *P. flexilis*). On the basis of its distinctive alar cell development *P. reesei* seems more closely related to *P. cuspidans* than to either *P. mauiensis* or *P. flexilis*.

6. *Pilotrichella vermiformis* Allen & Magill, *sp. nov.*

TYPE: Peru. Dept. San Martin, Prov. Rioja, Strasse Chachapoyas-Moyobamba km 397, w-exponierter Hang im Bergregenwald auf Sandstein, 1500 msm, 30 August 1982, *J.-P. Frahm*, *P. Geissler*, *S. R. Gradstein*, *G. Philippi*, *W. Schultze-Motel* 196 (holotype B, isotypes H, MO, NY).

Species haec a *P. flexili foliis* brevioribus cum superis marginibus breviter incurvis differt.

Plants small to medium-sized, dull, light green to brown-green, in loose, pendent mats. Primary stems not seen. Secondary stems long, trailing, and often pendent, to 12 cm long, irregularly branched, branches numerous, short or elongate, the elongate branches identical to the secondary stems; in cross section sclerodermis with 4–5 small, thick-walled, reddish orange cells, cortex cells enlarged, firm-walled, pale yellow, central strand absent; axillary hairs reddish throughout, 3–5 cells long, basal cells 1–2, short, quadrate to subquadrate, upper cells 2–3, long-cylindrical; paraphyllia absent; pseudoparaphyllia absent, branch primordia with scale leaves; rhizoids sparse,

in circular clusters abaxially to the leaf insertions, dark-red, smooth to finely roughened, mostly not branched. Secondary stem and branch apices short and swollen; leaves broadly ovate to obovate, at times panduriform, not ranked, erect-spreading, margins incurved when dry, erect when wet, 1.2–1.6 mm long, concave, clasping at base, auriculate; apices acute to broadly rounded, mucronate, leaf tips straight or reflexed; margins shortly incurved to plane, entire to obscurely serrulate above; costa absent; leaf cells linear-flexuose, porose throughout, median cells $26\text{--}66 \times 3\text{--}5 \mu\text{m}$; basal cells shorter and broader, alar cells bulging in strongly differentiated excavate groups, subquadrate to short-rectangular, $14\text{--}20 \times 10 \mu\text{m}$, yellowish red. Perigonia gemmate, lateral on secondary stems and branches, to 1.0 mm long, outer perigonial leaves clasping at base, squarrose recurved above, to 1.0 mm long, inner perigonia leaves broadly ovate below, acuminate above, orange-red across the base, cells elongate-flexuose, porose throughout, costa absent; paraphyses and curved-cylindrical antheridia numerous. Perichaetia and sporophytes not seen.

Etymology. The specific epithet *vermiformis* refers to the turgid, worm-like appearance of its stems and branches.

Distribution. South America (Peru).

Illustration. Figure 9.

Ecology. Apparently epiphytic; 1500–1550 m.

Specimens examined. PERU. Huánuco: *Plowman & Schunke 11723A* (NY); San Martín: *Frahm et al. 186* (B, NY), *196* (B, H, MO, NY).

Pilotrichella vermiformis is a small to medium-sized species with turgid stems/branches, and short, often obovate leaves that are broadly rounded to mucronate at the apex. The species also characteristically has plane or weakly incurved upper leaf margins. The leaf apices of *P. vermiformis* are usually erect, especially those of the stem/branch apical buds, but some leaves have recurved apices. The presence of some leaves with recurved apices and alar cells that are restricted to small, bulging, excavate groups indicates *P. vermiformis* is close to *P. flexilis*. *Pilotrichella flexilis* is a larger plant than *P. vermiformis* and its upper leaf margins are much more broadly incurved. *Pilotrichella vermiformis* is similar in size to *P. mascarenica*, but that species has narrower, more abruptly acute leaves, and strongly incurved upper leaf margins that commonly overlap below the apex.

Type not seen.

Pilotrichella thunbergii (Brid.) Jaeg., Ber Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 258. 1877. *Hypnum thunbergii* Brid., Muscol. Recent. 2(2): 172. 1801. *Isothecium thunbergii* (Brid.) Brid., Bryol. Univ. 2: 381. 1827. *Meteorium thunbergii* (Brid.) Mitt., J. Linn. Soc., Bot. 12:

432. 1869. Protologue: Jamaica. In Jamaica habitat, unde Cel. *Thunbergius* ad Jussioeum anno 1788 misit.

Wijk et al. (1967) make this a synonym of *Pilotrichella flexilis* on the authority of Crum and Steere (1957). In fact, Crum & Steere (1957) and Crum & Bartram (1958) list this taxon as a synonym of *Orthostichella hexasticha* (Schwaegr.) Buck. The protologue for *Hypnum thunbergii* indicates the plant came from Jamaica, and it has double costate, six-ranked leaves. These features indicate the taxon does not belong in *Pilotrichella*. *Orthostichella hexasticha* has never been collected in Jamaica, and it seems likely *Hypnum thunbergii* is an older species name for *Orthostichidium guyanense* (Mont.) Broth. The type of *Hypnum thunbergii* Brid. is not present at B, it may be at PC.

Excluded species

1. *Pleurozium quitense* (Mitt.) Allen & Magill, *comb. nov.*

Meteorium quitense Mitt., J. Linn. Soc., Bot. 12: 439. 1869. *Pilotrichella quitensis* (Mitt.) Jaeger, Ber. Thätigk. St. Gallischen Naturwiss Ges. 1875–76: 257. 1877. Protologue: Ecuador. Andes Quitenses, Jameson; in monte Pichincha (11,000 ped.), Spruce n. 1042. Lectotype (designated here): Ecuador. Andes Quitense in monte Pichincha (11,000 ped), Spruce 1042 (BM); isolectotypes: And. Quito (ad terram mihi videtur!), Spruce 1042 (H), Pichincha, Spruce s.n. (NY); syntype: Pichincha, S. A., Jameson s.n. (NY).

Hypnum quitense Mitt. In: Spruce, Cat. Musc. 15. 1867, invalid name, lacks a description.

Lembophyllum bolivianum Herz., Biblioth. Bot. 87: 123. 1916. Protologue: Bolivia. Zwischen Gras in der Felsschlucht von Toncoli, ca. 3500 m, N^o 4382 [Herzog]; an der Waldgrenze des Rio Saujana ca. 3500 m, N^o 3250/a [Herzog]. Types not seen, synonymized by Churchill & Linares (1995).

Plants medium to large-sized, dull, light green to brown-green, in loose mats. Primary stems creeping. Secondary stems long and spreading, to 15 cm long, irregularly branched, branches short or elongate, 1–2 cm long, often attenuate or ending in flagellate tips; in cross section sclerodermis with 3–5 small, thick-walled, yellow to reddish orange cells, cortex cells enlarged, thin-walled, pale yellow, central strand present; axillary hairs 4–5 cells long, basal cells 2, short, subquadrate, reddish, upper cells 2–3, long-cylindrical, hyaline; paraphyllia absent; pseudoparaphyllia absent, branch primordia with scale leaves; rhizoids sparse, generally on the parts of the stems that touch the substrate, in circular clusters abaxially to the leaf insertions, dark-red, smooth, mostly not branched. Secondary stem and branch apices short and

swollen; leaves broadly ovate to obovate, at times panduriform, not ranked, loosely erect with margins erect to broadly incurved when dry, erect when wet, 1.2–2.0 mm long, concave, clasping at base, variously auriculate; apices broadly acute to obtuse-rounded, leaf tips straight; margins broadly incurved above, serrulate at base, serrulate to serrate above and across the apex; costae short, indistinct, double or single; leaf cells linear-flexuose, apical cells 8–20 × 3–4 μm long, not porose, median cells 30–60 × 3–4 μm , smooth or weakly porose, basal cells porose, alar cells strongly differentiated in bulging, excavate groups, subquadrate to short-rectangular, partially bistratose, 4–5 μm × 6–8 μm , thick-walled, golden yellow, yellowish red, or brown. Dioicous. Perigonia not seen. Perichaetia lateral on secondary stems, to 2.0 mm long, perichaetial leaves erect-clasping at base, outer leaves, recurved above, broadly rounded to obtuse, to 1.0 mm long, inner leaves acuminate above, to 1.6 mm long, orange-red across the base, cells elongate-flexuose, porose at base, smooth above, costa absent; paraphyses and archegonia numerous. Setae elongate, 22–28 mm long, smooth, red. Capsules exserted, erect to slightly inclined above, long-cylindrical, 2.5 mm long; exothecial cells subrectangular, oblong, or rectangular, firm-walled; stomata superficial on neck; immature operculum rostrate, 1 mm long; annulus not seen; peristome diplolepidous, exostome yellow-brown, narrowly triangular, to 0.5 mm long, dorsal (outer) surface horizontally striate in lower ; with thick papillae above, median line and trabeculae thin at base, very thick in upper 1 of tooth. ventral (inner) surface smooth to lightly papillose, trabeculae thin, somewhat projecting, endostome yellow, lightly papillose, basal membrane high, segments broad, perforated, cilia not seen. Immature calyptra cucullate, smooth, 4 mm long. Spores spherical, lightly roughened, 16–24 μm .

Etymology. The specific epithet *quitense* refers to Quito, Ecuador, the region from which the type of the species was collected.

Distribution. South America (Ecuador, Peru, Bolivia).

Illustrations. Herzog (1916, Fig. 53, as *Lembophyllum bolivianum*).

Ecology. On tree and shrub trunks, soil banks, stones in creek, and at the base of cliffs; 2800–4000 m.

Selected specimens examined. ECUADOR. Cotopaxi: Dorr & Barnett 6265 (NY); Pichincha: Benoist 3263 (S). PERU. Ancash: (Prov. Yungay) Hegewald & Hegewald 7598 (MO); Ayacucho: Frahm 823916a (B); Cajamarca: (Prov. Cajamarca) Sagástegul 10297 (MO), (Prov. Contumazá) Hegewald & Hegewald 7316 (MO), (Prov. Hualgayóc) Raimondi 3093 (B); Cusco: (Prov. La Convencion) Bües 1471 (MO); La Libertad: (Prov. Otuzco) Hegewald & Hegewald 7167 (H, MO). BOLIVIA. La Paz: (Prov. Inquisivi) Lewis 38580

(MO, NY), (Prov. Larecaja) Lewis 83-172 (H, MO, NY), (Prov. Saavedra) Lewis 79-1046 (MO).

Pleurozium quitense occurs on humus or soil on the ground, over rocks and at the bases of trees. It has somewhat tumid, often attenuate stems and branches. Its leaves are broadly concave, have serrulate leaf margins, linear-flexuose cells, and short double (rarely single) costae. An especially critical feature of the species is the presence of a stem central strand. Sporophytically *P. quitense* has long setae, erect to slightly inclined cylindrical capsules and a standard hypnoid peristome.

This species has long been known as *Pilotrichella quitensis*, but its standard hypnoid peristome as well as leaves with short double costae, stems with a central strand, and its terrestrial habitat preference make it impossible to place the species in *Pilotrichella*. The taxon could perhaps be accommodated in *Weymouthia* since all of the important features of *Pleurozium quitense* are found in *Weymouthia* except for one; *Weymouthia* stems lack a central strand. *Acrocladium* is a south temperate genus with the same habitat preference as *P. quitense*, a similar peristome, and stems that have a central strand. The leaves of *Acrocladium* differ from those of *P. quitense* in having short, single costae, and inflated, thin-walled alar cells.

The genus *Pleurozium* is usually considered to have a single species, *P. schreberi* (Brid.) Mitt, which is common in the north temperate regions and also present in northern South America. *Pleurozium quitense* and *P. schreberi* have the same habitat preference and stems with central strands. Furthermore, both species have attenuate branches and similar leaf forms, leaf areolation, alar cell development, costa form, seta length, capsule shape, operculum form, and peristome structure. *Pleurozium quitense* differs from *P. schreberi* in having more or less erect capsules, yellowish to dull red rather than dark red, glossy stems, and more strongly developed attenuate branches. In addition, the leaves of *P. quitense* are turgid when dry, while those of *P. schreberi* are often somewhat flattened with narrower, more or less acuminate branch leaves that are curved to spreading when dry.

Mitten seems to have had some idea of associating *Pilotrichella quitense* with *Pleurozium*. The sheet bearing the syntypes of *Meteorium quitense* at NY came from the Mitten Herbarium and was annotated by R. S. Williams with the words "Found with *H. schreberi*." Williams considered the syntypes of *Meteorium quitense* to belong to *Weymouthia*. It is of interest to note that Hermann (1976) synonymized *Lembophyllum bolivianum* with *Pleurozium schreberi*.

2. *Pilotrichella flexilis* var. *gracilis* Broth. & Par. In: Thér., Trav. Bryol. Déd. P.-T. Husnot 2 [14]: 19. 1944. Invalid name, no description given.

Based on: Haiti, Croix-des-Bouquets, Badeau, 1,300–2,000 m. [Ekman] (N^o 7666 pp.). Haiti: Massif de la Selle, Croix-des-Bouquets, Badeau, slope towards Camp-Franc, 1300 m, 22.II.1927, leg. E. L. Ekman 7666 (S). = *Squamidium nigricans* (Hook.) Broth.

3. *Pilotrichella serricola* C. Müll. In: Paris, Index Bryol. 949. 1897. Invalid name, no description given. Based on: Ule Bryoth. brasil. n. 67. E. Ule: Bryotheca Brasiliensis, N^o 67. Prov. Santa Catharina: Serra Geral, Junii 1890, leg. E. Ule (BM). = *Squamidium brasiliense* (Hornsch.) Broth.

New distributional records

1. *Camptochaete arbuscula* (Reicht.) Broth.

There is a collection in NY, previously named *Pilotrichella mauiensis*, of *Camptochaete arbuscula* (Reicht.) Broth. The collection label gives no collector or collection number, and gives the locality only as "Sandwich Islands" (= Hawaii). The only other species of *Camptochaete* in Hawaii is *C. pulvinata* (Hook. & Wils.) Jaeg. (see Bartram 1933). *Camptochaete arbuscula* is otherwise found in southeastern Australia and New Zealand (Tangney 1997).

2. *Weymouthia mollis* (Hedw.) Broth.

There are two collections of this species at F from Tahiti (Hab. troncos de montagne, 1896, Nadeaud), and one collection of it at L from the Falkland Islands (Ad. ins. Maclov. (Falklandii) orient. sinum Port William Standley, Sept. m, W. Lechler pl. ins. Maclovian, Ed. R. F. Hohenacker). *Weymouthia mollis* has previously been reported from the Australian mainland, Tasmania, Lord Howe Island, New Zealand, the Juan Fernandez Islands, and Chile.

Acknowledgement

This research was funded by the U.S. National Science Foundation through a grant to the Missouri Botanical Garden (DEB 9522034 PEET). The curators of herbaria providing loans or access to collections are gratefully acknowledged (B, BM, F, FH, G, H, J, L, NY, PC, S, US). We thank William R. Buck and Marshall Crosby for nomenclatural assistance and for sharing their views on *Pilotrichella*. Special thanks are due to Len Ellis, Heidemarie Nowak-Krawietz, and Ronald Pursell for help in locating type material. Steve Churchill, Chris Casado, Zacharia Magambo, and Michelle Price provided logistical support to this study. We are indebted to Peter H. Raven for his strong support and continued encouragement of the bryological program at the Missouri Botanical Garden.

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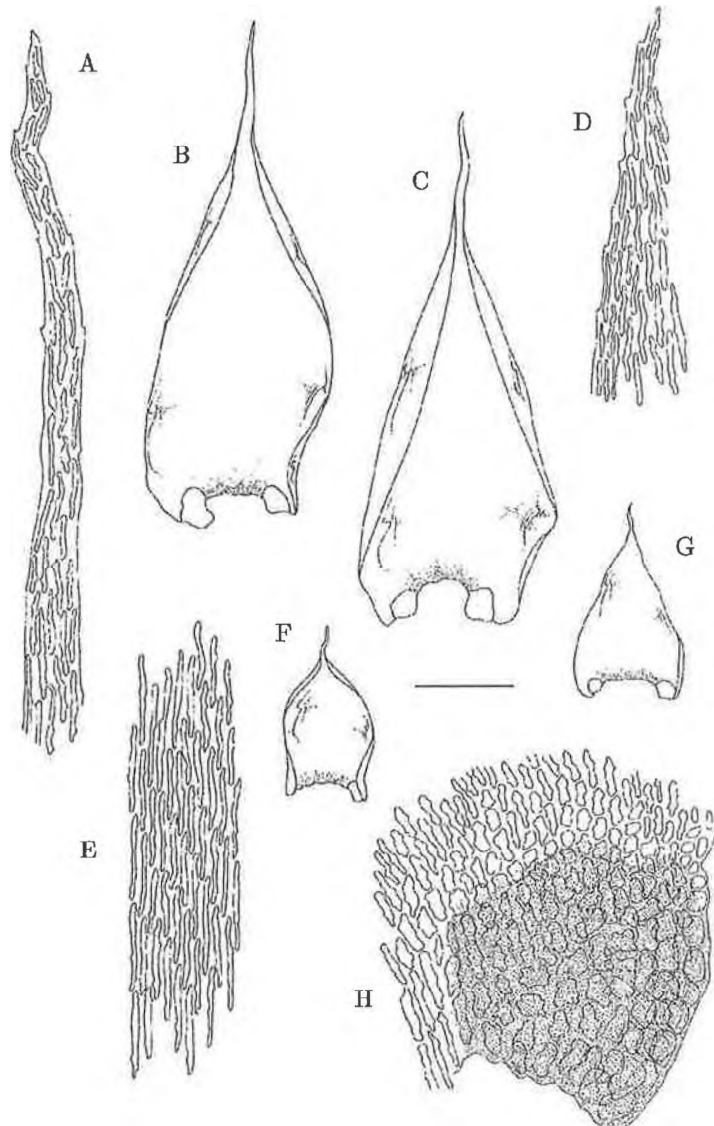


Figure 1. *Pilotrichella cuspidans*. A. Leaf apex. B & C. Branch and stem leaves. D. Upper leaf margin. E. Median leaf cells. F & G. Primary stem leaves. H. Alar cells. Scale in mm: bar = 0.06 (A, D, E, H); bar = 0.5 (B, C, F, G). Figures A-E, H from Duncan 28; figures F & G from Zanoni 30375.

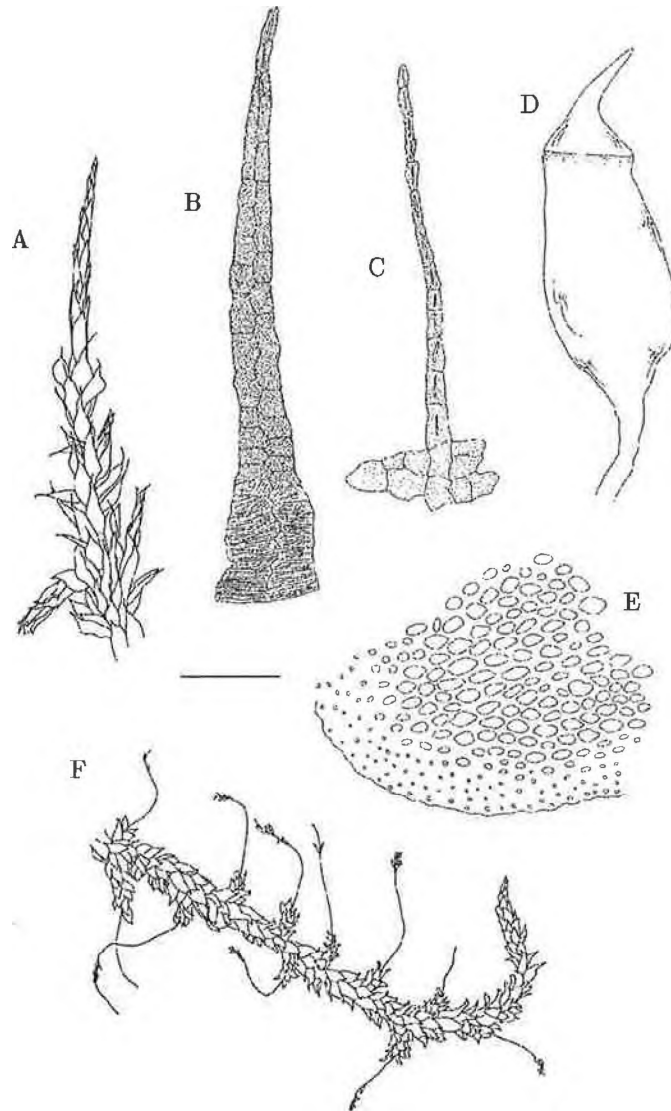


Figure 2. *Pilotrichella cuspidans*. A. Habit. B. Exostome tooth, dorsal (outer) surface. C. Endostome segment and part of basal membrane, ventral (inner) surface. D. Capsule and operculum. E. Stem cross section. *Pilotrichella flexilis* form *nudiramulosa*. F. Habit. Scale in mm: bar = 0.08 (B, C, E); bar = 0.6 (D); bar = 3.3 (A); bar = 5.1 (F). Figure A from Steere 22825; figures B-D from Buck 8304B; figure E from Bolay 92; figure E from the type; F from the type.

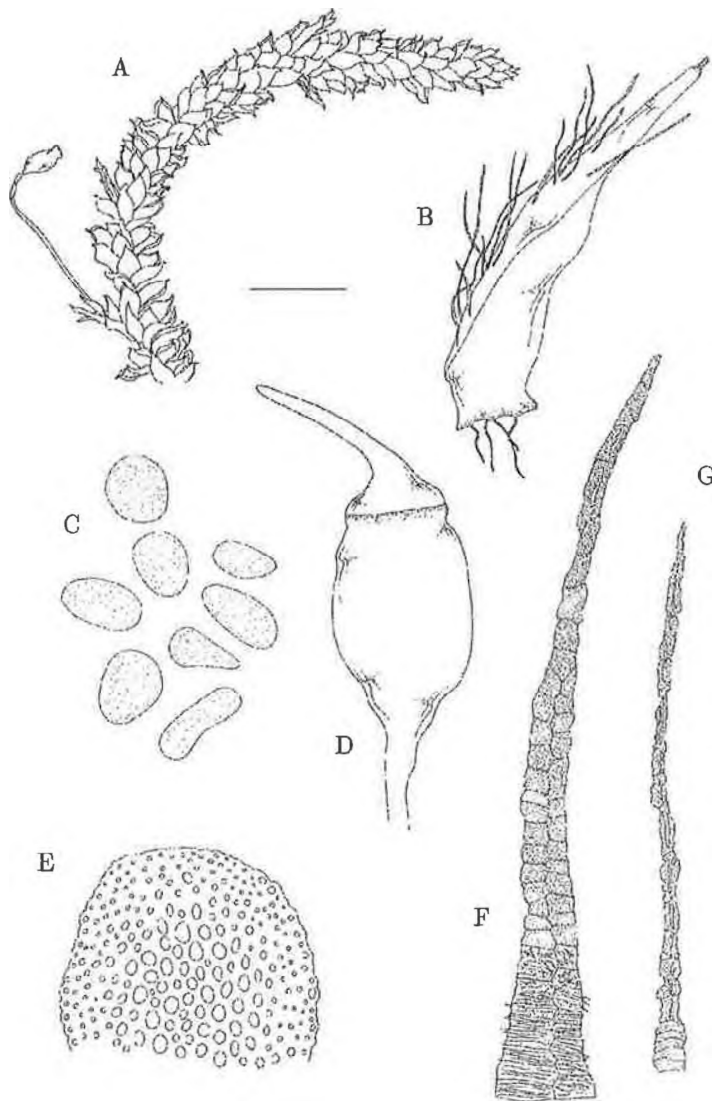


Figure 3. *Pilotrichella flexilis*. A. Habit. B. Calyptra. C. Spores. D. Capsule and operculum. E. Stem cross section. F. Exostome tooth, dorsal (outer) surface. G. Endostome segment, ventral (inner) surface and part of basal. Scale in mm: bar = 0.08 C & E); bar = 0.09 (F & G); bar = 0.71 (B & D); bar = 5.1 (A). Figures B & D from Britton 100; Figures A, C, E-G from Allen 11549.

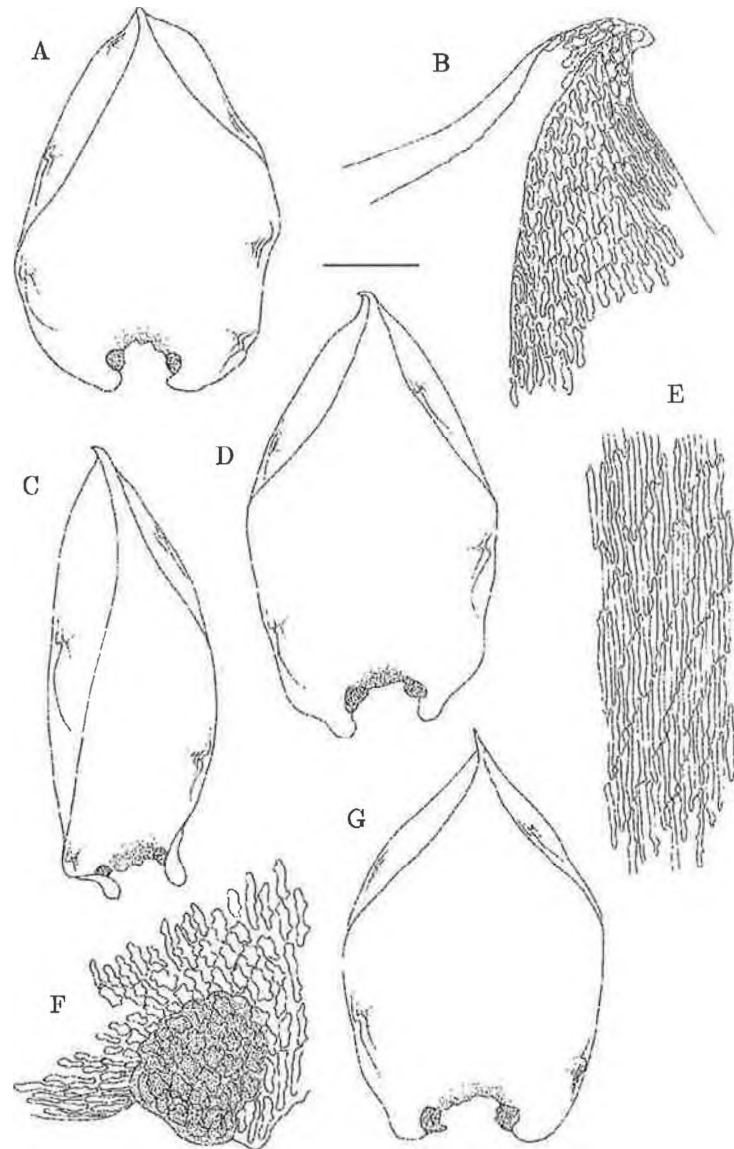


Figure 4. *Pilotrichella flexilis*. A, C, D, G. Leaves. B. Leaf apex and upper margin. E. Median leaf cells. F. Alar cells. Scale in mm: bar = 0.06 (B, E, F); bar = 0.5 (A, C, D, G). Figure A from Pócs & Mwanjabe 6467D (Tanzania); Figures B–F from Allen 11549 (Honduras); Figure G from Pócs 9011/W (Cuba).

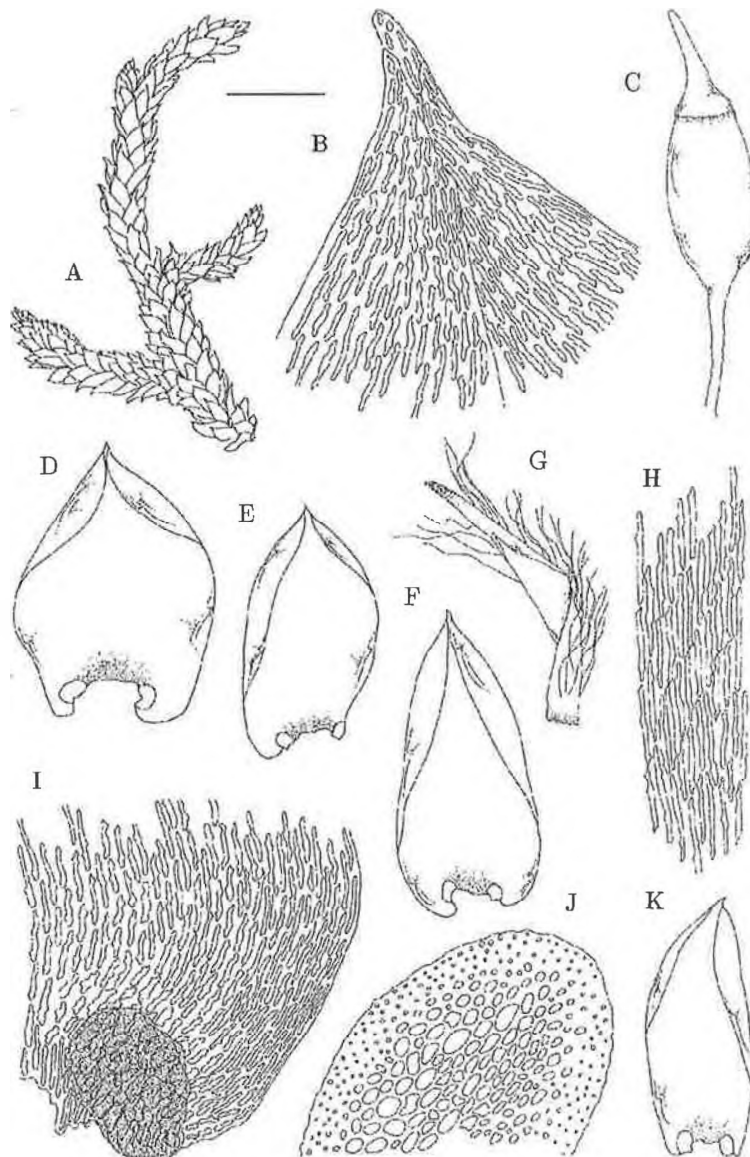


Figure 5. *Pilotrichella mascarenica*. A. Habit. B. Leaf apex and upper margin. C. Capsule and operculum. D. Stem leaf. E, F, K. Branch leaves. G. Calyptra. H. Median leaf cells. I. Alar cells and basal leaf margin. J. Stem cross section. Scale in mm: bar = 0.06 (B, H, I); bar = 0.08 (J); bar = 0.51 (C-F, K); bar = 1.3 (G); bar = 2.6 (A). Figures A, D, E, J from Crosby & Crosby 9006; figures B, H, F, I from the type; figures C, G from Crosby & Crosby 5272; Figure K from Borgen 30.

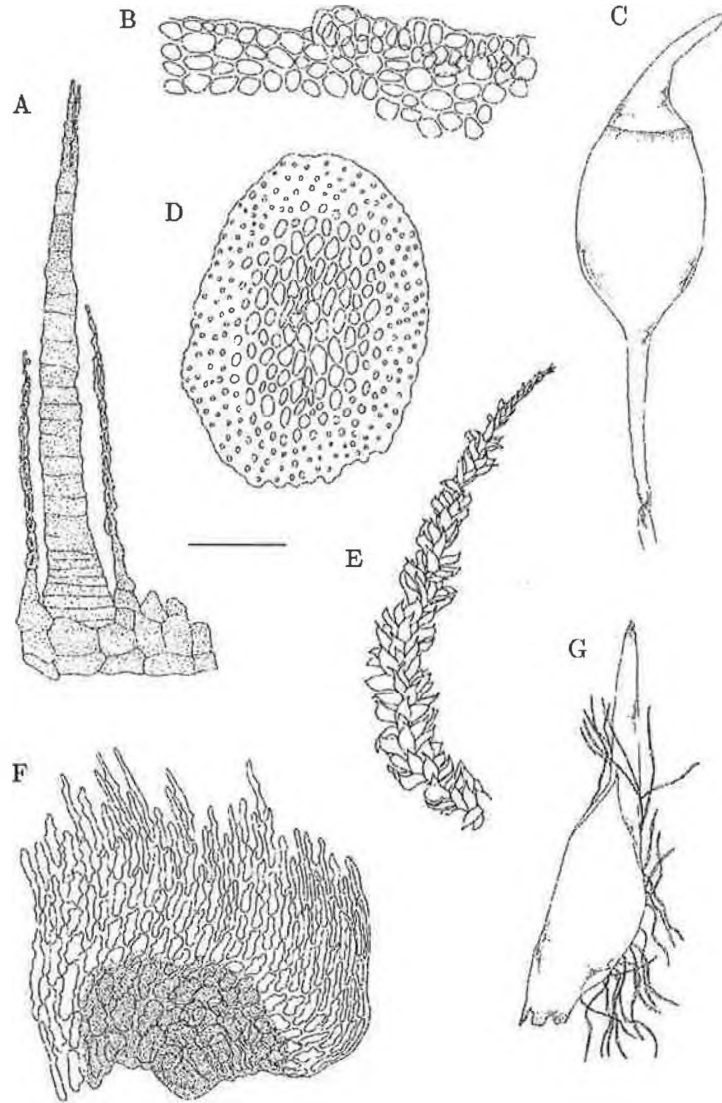


Figure 6. *Pilotrichella mauiensis*. A. Exostome tooth, two endostome segments, and part of basal membrane, ventral (inner) surface. B. Capsule mouth with rudimentary annulus. C. Capsule and operculum. D. Stem cross section. E. Habit. F. Alar cells and basal leaf margin. G. Calyptra. Scale in mm: bar = 0.06 (B, D, F); bar = 0.09 (A); bar = 0.9 C & G); bar = 2.7 (E). Figures A-C, G from Pringle 10417; figure D from the type; figure E from *Bryophyta Hawaiica Exsiccata* 37; Figure F from Allen 17364.

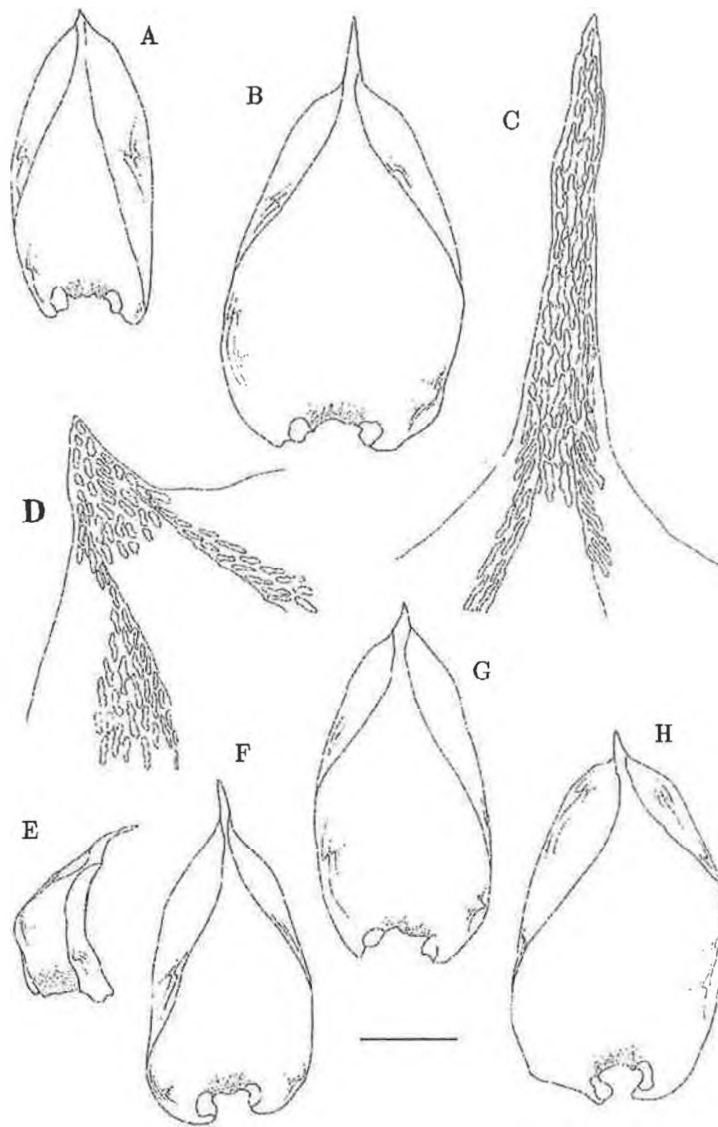


Figure 7. *Pilotrichella mauiensis*. A, B, F-H. Leaves. C & D. Leaf apices. E. Primary stem leaf. Scale in mm: bar = 0.06 (C & D); bar = 0.40 (A, B, E-H). Figures A & D from the type (Hawaii); figures B & C from Allen 17364; figures E & G from *Bryophyta Hawaiica Exsiccata 37* (Hawaii); figure F from Hermann 28836 (Mexico); figure H from Pringle 10417 (Mexico).

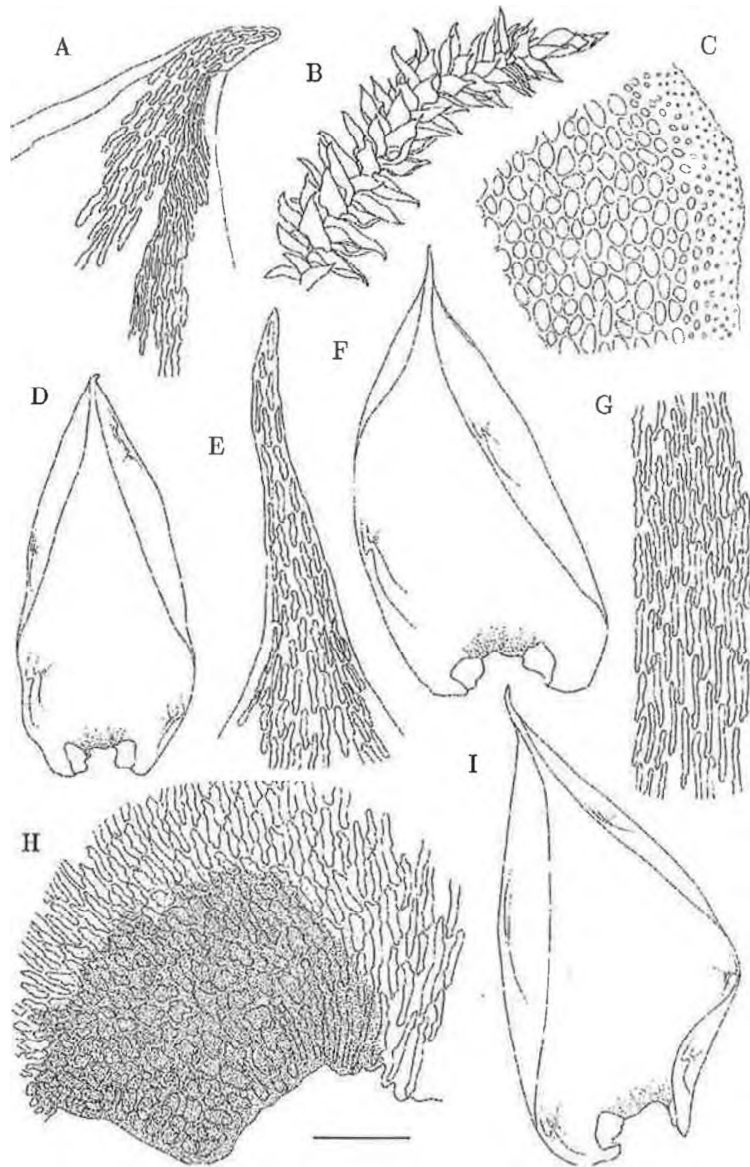


Figure 8. *Pilotrichella reesei*. A. Leaf apex and upper margin. B. Habit. C. Stem cross section. D, F, I. Leaves. E. Leaf apex. G. Median leaf cells. H. Alar cells. Scale in mm: bar = 0.06 (A, E, G, H); bar = 0.08 (C); bar = 0.5 (D, F, I); bar = 3.2 (B). All figures from the type.

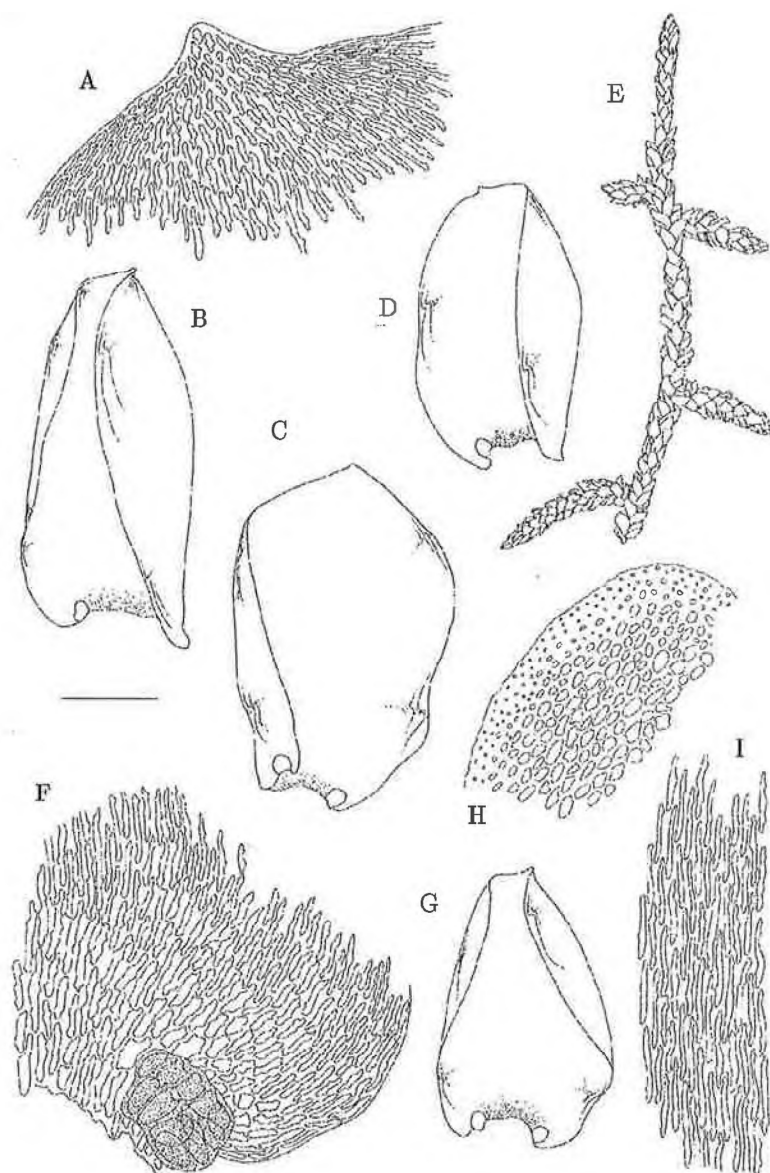


Figure 9. *Pilotrichella vermiformis*. A. Leaf apex. B & C. Stem leaves. D & G. Branch leaves. E. Habit. F. Alar cells and basal margin. H. Stem cross section. I. Median leaf cells. Scale in mm: bar = 0.06 (A, F, I); bar = 0.08 (H); bar = 0.5 (B-D, G); bar = 5.0 (E). All figures from the type.