

A Taxonomic Revision of the Propaguliferous Species of *Pohlia* (Bryaceae, Bryophyta) in Latin America

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► Resumen — Suárez, Guillermo M. & Schiavone, María M. 2011. "Revisión Taxonómica de las especies propaguliferas de *Pohlia* (Bryaceae, Bryophyta) en América Latina". *Lilloa* 48 (2). Se presenta un estudio taxonómico y descriptivo de las especies propaguliferas de *Pohlia* en Centro y Sud América. Seis especies con yemas axilares y una con propágulos rizoidales son reconocidas en el área de estudio. *Pohlia richardsii* de Costa Rica es un nuevo sinónimo de *P. apolensis*. *Pohlia longipedicellata* de Venezuela y *P. verrucosa* de Bolivia son nuevos sinónimos de *Pohlia papillosa*. La identidad de *Bryum anisodontacum nom. nud.*, de Chile es clarificada y este nombre es sinonimizado con *P. papillosa*. Nuevos lectotipos son propuestos. Se analizan caracteres de importancia taxonómica para las especies americanas de *Pohlia*.

Palabras clave: América, *Bryum*, propágulos, propágulos rizoidales, yemas, *Webera*.

► Abstract — Suárez, Guillermo M. & Schiavone, María M. 2011. "A taxonomic revision of the propaguliferous species of *Pohlia* (Bryaceae, Bryophyta) in Latin America". *Lilloa* 48 (2). A taxonomic and descriptive study of the propaguliferous species of the genus *Pohlia* with axillary and rhizoidal bulbils from Central and South America is presented. Six species with axillary gemmae and one with rhizoidal tubers are recognized in the study area. *Pohlia richardsii* from Costa Rica is a new synonym of *P. apolensis*. *P. longipedicellata* from Venezuela and *P. verrucosa* from Bolivia are new synonyms of *P. papillosa*. The identity of *Bryum anisodontacum nom. nud.*, from Chile is clarified and this name is placed in synonymy with *P. papillosa*. New lectotypes are proposed. Taxonomically important characters of American *Pohlia* species are reviewed.

Keywords: America, *Bryum*, bulbils, gemmae, propagula, tubers, *Webera*.

INTRODUCTION

The genus *Pohlia* Hedw. is represented by 16 species in Central and South America (Suárez & Schiavone, 2010). In North America nine species have asexual reproduction by propagula (Shaw, 1981); in Europe, this group comprises ten species and two varieties (Hill *et al.*, 2006).

In Latin America, seven species with axillary [*P. apolensis* R.S. Williams, *P. australis* A.J. Shaw & Fife, *P. drummondii* (Müll. Hal.) A.L. Andrews, *P. lonchochaete* (Dusén) Broth., *P. papillosa* (Müll. Hal. ex A. Jaeger) Broth. and *P. pseudobarbula* (Thér.) H.A. Crum & A.J. Shaw] or rhizoidal [*P. wilsonii* (Mitt.) Ochyra] propagula are recognized. Among the propaguliferous species, *P.*

lonchochaete presents the most distinctive propagula (Suárez & Schiavone, 2010), which are more homogeneous among the other species.

The present article provides morphological, ecological and taxonomic data that broaden the knowledge of these propaguliferous species in a territory where they are infrequent and probably undercollected. A summary of differential characters is presented for genus *Pohlia*.

MORPHOLOGY AND LIFE HISTORY OF *POHLIA* IN THE AMERICAS

The greatest morphological and species diversity of *Pohlia* is found in the Northern Hemisphere. As in other parts of the globe, including the Neotropics, species of this genus preferably occur at high elevations and

are distributed mainly along the Andean corridor. While all species grow on soil, the diversity of microhabitats in which they occur results in surprising morphological variability among species as well as within the species. This section summarizes aspects of distribution, habitat, general morphological and anatomical characters and those features that are of diagnostic value in the systematic treatment of *Pohlia*.

DISTRIBUTION

In the New World, North America has the highest species richness, with 30 recognized species (Shaw, 1982), while Latin America's diversity is rather low (Suárez, 2008; Suárez & Schiavone, 2010, 2011). Out of the approximately 36 specific names in *Pohlia*, only 16 species are accepted here. *Pohlia longicollis* (Hedw.) Lindb., *P. wahlenbergii* (F. Weber & D. Mohr) A.L. Andrews, *P. cruda* (Hedw.) Lindb., *P. nutans* (Hedw.) Lindb., *P. elongata* Hedw. and possibly *P. oerstediana* (Müll. Hal.) A.J. Shaw are cosmopolitan species (Suárez & Schiavone, 2010; Suárez & Ochyra, 2011), while *P. pseudobarbula*, *P. papillosa*, *P. apolensis*, *P. lonchochaete*, *P. magnifica* (Herzog) S. He and *P. salaminae* (Müll. Hal.) Broth., are found only in Latin America. In addition, species such as *P. chilensis* (Mont.) A.J. Shaw, *P. wilsonii* (Afro-American), *P. australis* and *P. tenuifolia* (A. Jaeger) Broth. (circumsubantarctic), grow on more than one continent. *Pohlia drummondii* has a disjunct distribution in the Americas and is only found in North America and in southern Chile and Argentina.

HABITS AND HABITATS

Pohlia is a genus of acrocarpous mosses, with erect stems, unbranched or with 1–4 subfloral innovations. In the Neotropics, the species grow predominantly in Andean habitats where they form dense turfs on the ground or in rock crevices. However species such as *P. magnifica* grow near glacier melt-water and *P. lonchochaete* is found in swampy environments.

These species generally grow in lax turfs and may occur down to the sea level. Like other

Pohlia, the Latin American species present great phenotypic plasticity as regards habit, size, arrangement of leaves, and colour of plants, usually in response to environmental conditions. The high Andean populations of *P. wahlenbergii* have short stems, hardly imbricate leaves, and a reddish colour, while the lowland plants have elongate stems, lax leaves, and are olive green. Similarly, in high Andean populations (Peru and Bolivia) of *P. cruda*, the plants are small, 1–2 cm high; when they grow under favorable conditions, however, plants are robust. On the other hand, *P. wilsonii* is an Afro-American species that has variations in life form, in response to micro-environmental conditions. In populations that grow packed together, they form dense or lax turfs, depending on, for example, light intensity or water availability. This morphological variation that is related to environmental differences has been given taxonomic recognition, usually at the varietal level. However, in agreement with Shaw (1982), this paper does not recognize infraspecific taxa.

STEMS

The colouration of the stems is a diagnostic character in species identification. The stems are generally reddish, except those of *Pohlia papillosa*, *P. oerstediana*, *P. apolensis*, *P. wilsonii* and some populations of *P. wahlenbergii*, which are green. In *P. drummondii* the reddish colouration is very intense, and the stem appears translucent. Anatomically, there are no differences of taxonomic value. The stems consist of three layers: epidermis, cortex and central strand region (Kawai & Ochi, 1987, type A). However, the degree of development of the central strand may vary depending on the species size (Figure 1).

AXILLARY HAIRS

No species has axillary hairs that are longer than 150 µm long, with 1–4 brown basal cells and 1–4 hyaline cells, although some species (*P. cruda*, *P. oerstediana*, *P. tenuifolia*, *P. pseudobarbula*, *P. chilensis* and *P. papillosa*) have more than four basal

brown cells. Among the taxa examined, the axillary hairs of *P. wahlenbergii* are the shortest ones.

LEAVES

The foliar characters are considered of diagnostic value not only to distinguish the genus from others ones in the Bryaceae but also to mark intraspecific differences (Figure 2). They are usually yellowish green, excep-

tionally red (*P. wahlenbergii*) or reddish brown (*P. salaminae*) in plants exposed to sunlight, or with an opaque or metallic sheen (*P. cruda*, *P. longicollis*, *P. drummondii*, *P. oerstediana*, *P. magnifica*, and *P. drummondii*). The leaves are arranged laxly along the stem, the apical ones being longer than the basal ones. The leaves in some plants are arranged densely in a coma (*P. chilensis* and *P. salaminae*, see Suárez &

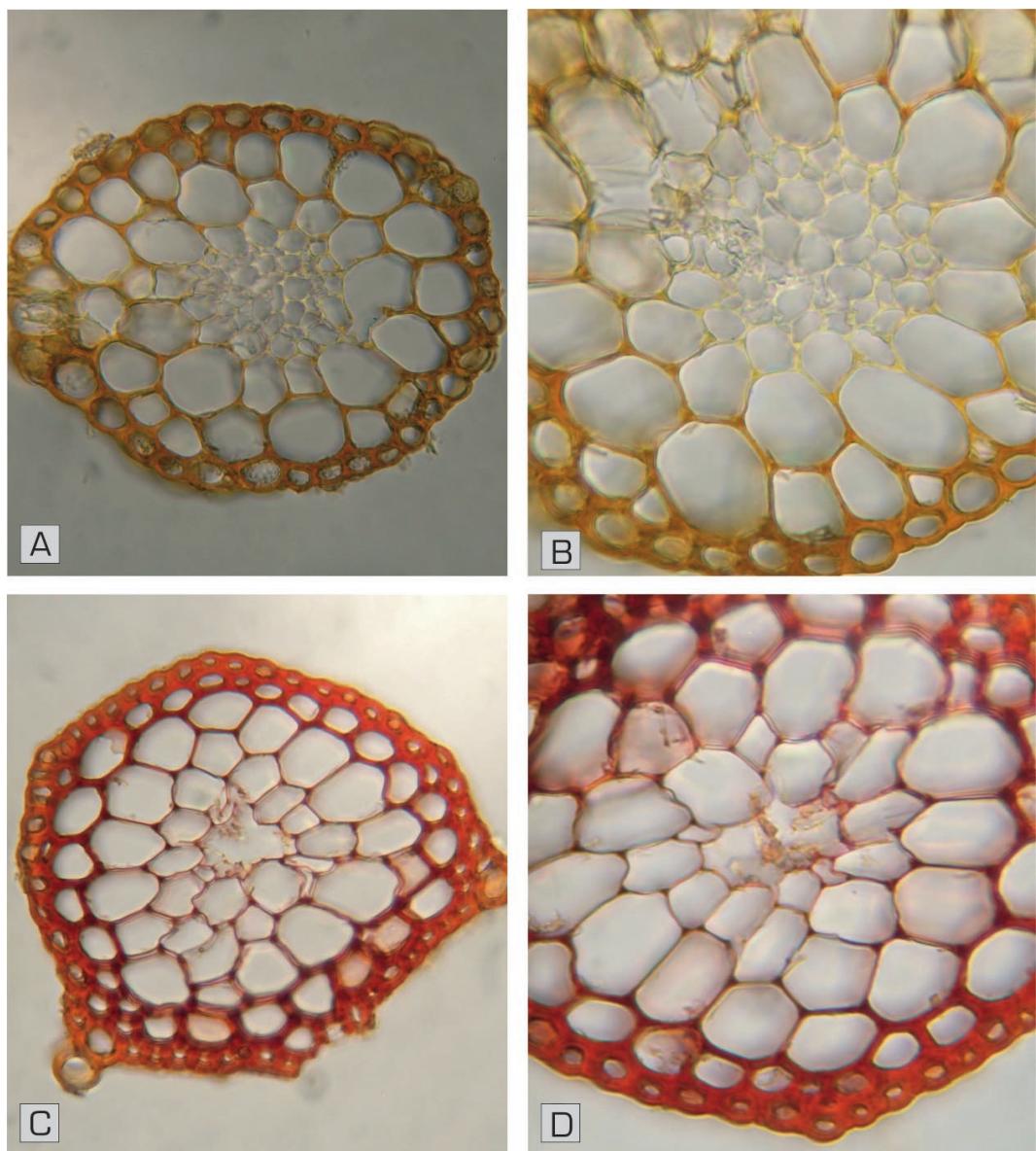


Figure 1. Cross section stems. A, B – *Pohlia wilsonii*; C, D – *P. wahlenbergii*.

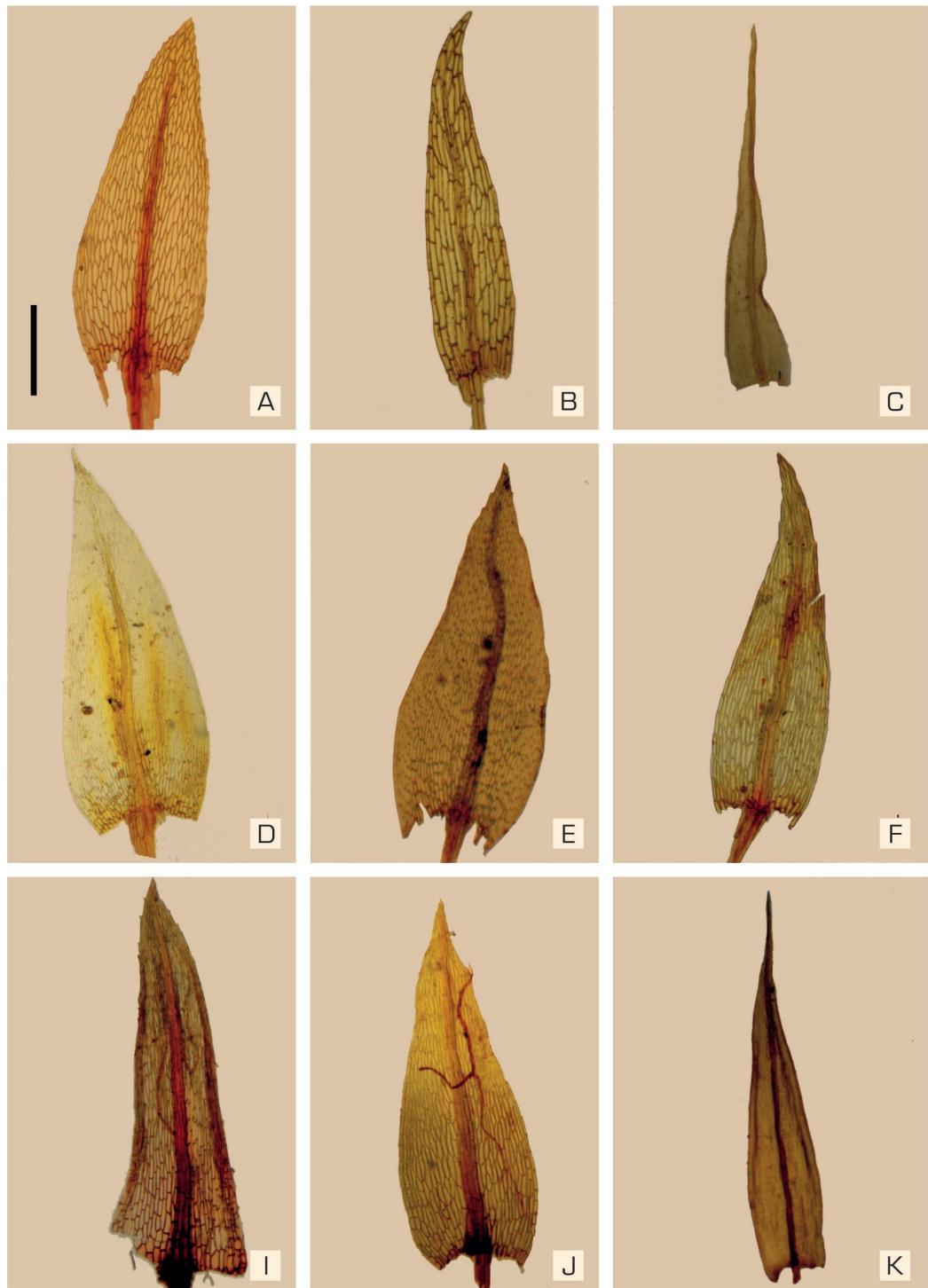


Figure 2. Leaf morphology. A – *P. wahlenbergii*; B – *P. wilsonii*; C – *P. tenuifolia*; D – *P. chilensis*; E – *P. drummondii*; F – *P. apolensis*; G – *P. salaminae*; H – *P. lonchochaete*; *P. magnifica*. Scale bars: A, I = 0.75 mm; B, C, H = 0.5 mm; D, E = 0.3 mm; F, G = 0.25 mm.

Schiavone, 2008a). In most species studied, the leaves are narrowly or broadly lanceolate, except in *P. tenuifolia*, where they are linear-lanceolate (Suárez, 2011). The margins are plane to slightly recurved, usually serrate to denticulate toward apex. The costa is single, percurrent or subpercurrent (ending 2–6 cells below the apex), exceptionally short excurrent (*P. nutans* and *P. lonchochaete*) or excurrent (*P. magnifica*, Suárez & Schiavone, 2010), red, reddish at the base only (propaguliferous species) or, less frequently, green (*P. chilensis*, *P. oerstediana* and *P. longicollis*). The anatomy of the costa is uniform, with a dorsal and ventral epidermis, 2–4 guide cells, a dorsal strand of hydroids and two layers of stereids, the ventral one being less well developed. The leaves are decurrent, and the degree of decurrency is relatively constant within each species. However, the leaf is usually more markedly decurrent when the leaf arrangement is lax. The upper and median leaf cells are long, fusiform or rhombic and thin-walled, except in *P. elongata*, *P. magnifica*, *P. lonchochaete* and *P. nutans*. The basal cells are generally short-rectangular (Figure 3 C, F1), whereas in some species they are markedly different and represent a specific character. While the leaves of the South American species are relatively uniform, the combinations of leaf characters are useful for species identification.

PROPAGULA

Of the 16 South American species of *Pohlia*, six reproduce asexually through propagula. In most species, the size of the propagula is uniform, the smallest (150 µm) being found in *P. papillosa* and *P. apolensis*. They are always in leaf axils, usually appear in groups, but in *P. drummondii* and *P. lonchochaete* there is only one propagulum per leaf axil. Mostly, all the leaves axes of the plant are propaguliferous, but Andean *P. drummondii* has only one or few propaguliferous leaves. Sterile *P. papillosa* has abundant propagula only in the distal leaves. The propagula are usually coloured but depending on the intensity of the colour, they may

appear translucent or opaque as in *P. lonchochaete* (Suárez & Schiavone, 2010). Variation in colour has been observed in *P. apolensis*, where young propagula are hyaline, but mature ones are red. The propagula are attached in the leaf axils by a uni- or multicellular, hyaline, usually deciduous gemmophores (in *P. lonchochaete* they are sessile). The propagulum body consist of a mass of isodiametric or linear cells, with thin walls and leaf primordia (absent in *P. lonchochaete*) on the apex or the whole body of the propagulum. Within the species the propagulum morphology is usually homogeneous, but young propagula of *P. pseudobarbula* are more rounded than mature ones. Those of *P. apolensis* are more elongate and hyaline when young and become rounded-oblong and red at maturity. The morphological variation of the propagula is related to the shape and distribution of the leaf primordia. Among the South American propaguliferous species propagula can be oblong, with laminar leaf primordia distributed over the body (*P. pseudobarbula*, *P. drummondii*, *P. australis*), rounded to oblong with leaf primordia uncinate and arranged apically (*P. apolensis*), oblong-triangular without leaf primordia (*P. lonchochaete*), or oblong (*P. papillosa*) or in Andean plants, vermicular with apical laminar leaf primordia.

PERICHAETIAL LEAVES

The modified leaves that surround the archegonia of the South American species are morphologically similar to vegetative leaves (Figure 4), but sometimes they differ in larger size. They are mostly not considered to be of taxonomic value, but in *P. wilsonii* the perichaetal leaves are conspicuously longer than the vegetative ones. In this character it resembles *P. longibracteata*, a Northern Hemisphere species. All polysetous species of *Pohlia* have perichaetal leaves that are poorly differentiated from vegetative ones.

PERIGONIAL LEAVES

The morphology of the perigonial leaves is uniform among South American species,

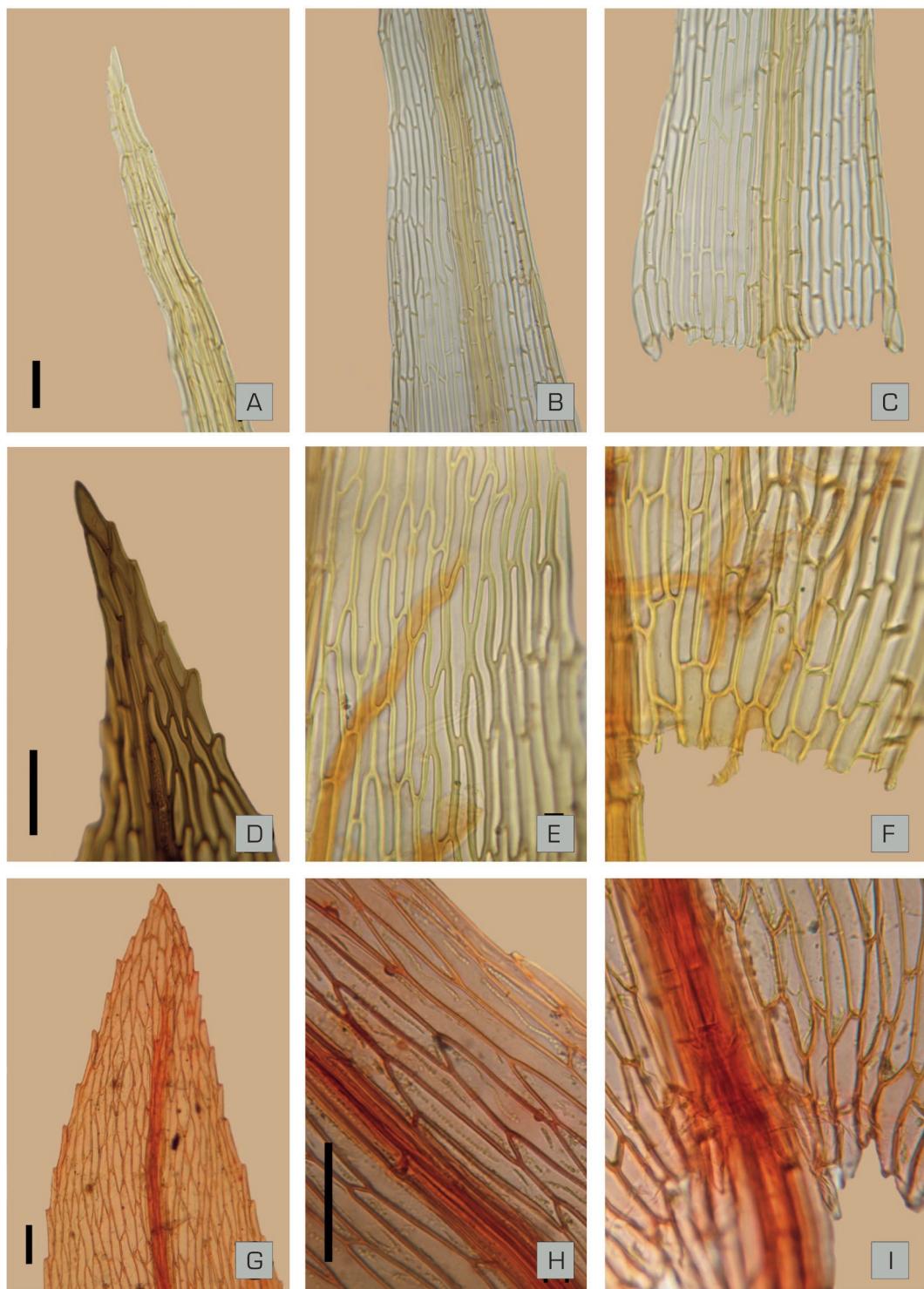


Figure 3. *P. tenuifolia*: A – Apex, B – Median cells, C – Basal cells; *P. nutans*: A – Apex, B – Median cells, C – Basal cells; *P. wahlenbergii*: A – Apex, B – Median cells, C – Basal cells. Scale bars: A-C = 50 µm; D-G = 40 µm; H-I = 50 µm.

ranging from oblong to oblong-cuspidate and acuminate. The largest ones were observed in *P. cruda* (4 mm).

SETAE

The seta is simple and erect, with the exception of polysetous species (Suárez & Schiavone, 2008a), which have two or more flexuose and helically twisted setae per perichaetium. The length of the seta is rather constant within species; although, differences were observed between montane and Andean populations of *P. papillosa* and *P. chilensis*, where the mountain plants have longer setae. The anatomy of the seta is similar to that of the stem,

although most cells have more thickened walls than the stem (Figure 5).

CAPSULES

Most South American species have inclined, cylindrical capsules with distinct necks. However, the propaguliferous species (*P. apolensis*, *P. drummondii*, *P. papillosa* and *P. longochaete*) and *P. magnifica* are characterized by erect to inclined, pyriform capsules. In *P. wahlenbergii* the dried capsule is erect and urceolate without a distinct neck, however when fresh, the neck is almost as long as the urn (Shaw, 1982). The relationship between neck and urn length has been used for inters-



Figure 4. Perichaetial leaves: A – *P. papillosa*; B – *P. drummondii*; C – *P. apolensis*. Perigonial leaves: D – *P. chilensis*; E, F – *P. papillosa*. Scale bars = 0.5 mm.

pecific differentiation. Moreover, the length of the capsules can distinguish *P. elongata*, the only one in the genus reaching 7 mm.

EXOTHECIAL CELLS

Exothecial cell shape and cell wall thickness are important characteristics for infrageneric differentiation within *Pohlia* (Figure 6). Exothecial cells vary from nearly rectan-

gular to isodiametric with walls thickened, straight or sinuous, and often collenchymatous (*P. wahlenbergii* and *P. drummondii*). Only *P. papillosa* and *P. apolensis* display bulging walls.

STOMATA

The stomata are restricted to the neck area of the capsule. In most South American

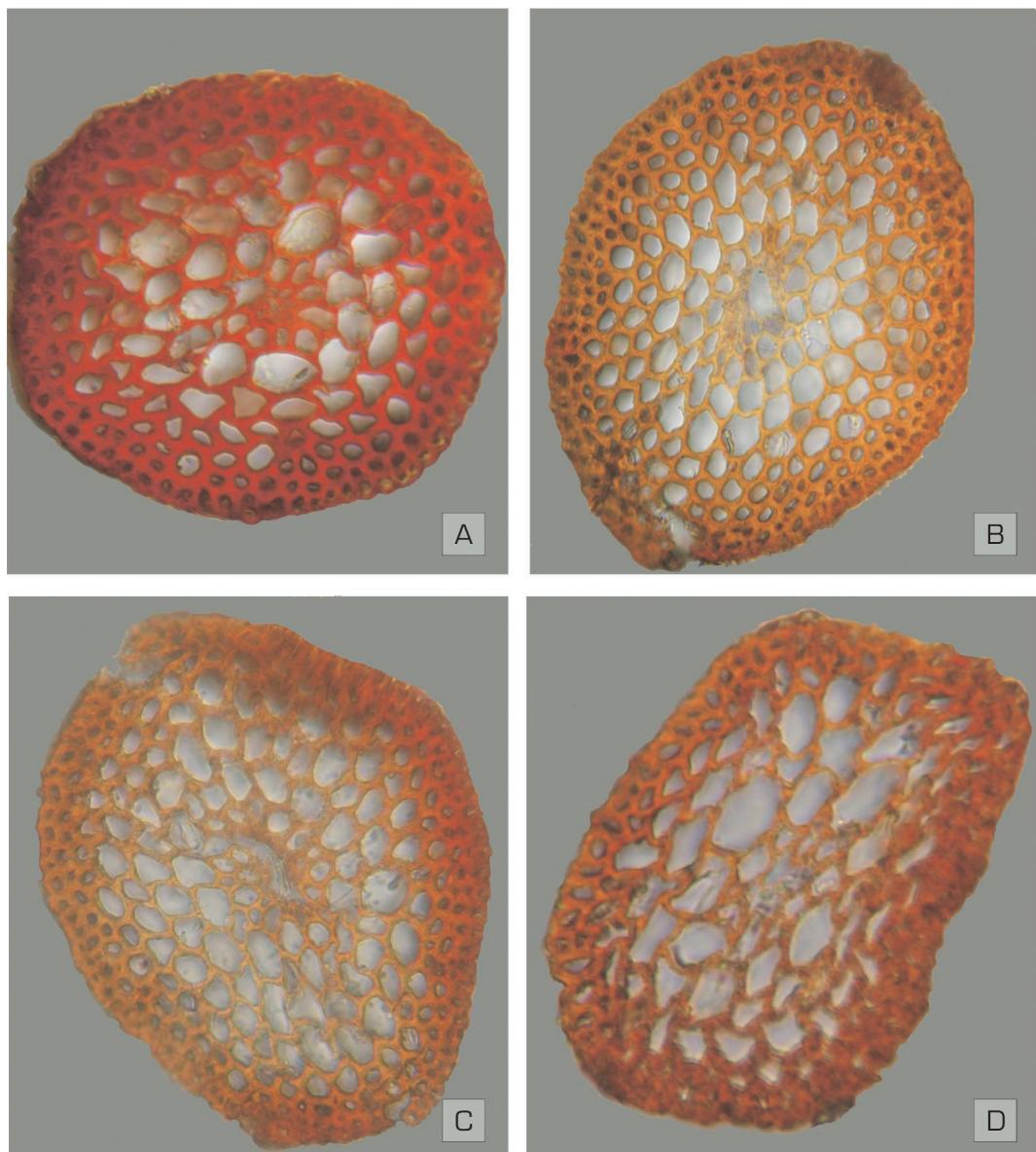


Figure 5. Cross section setae. A – *P. chilensis*; B – *P. cruda*; C – *P. elongata*; D – *P. tenuifolia*.

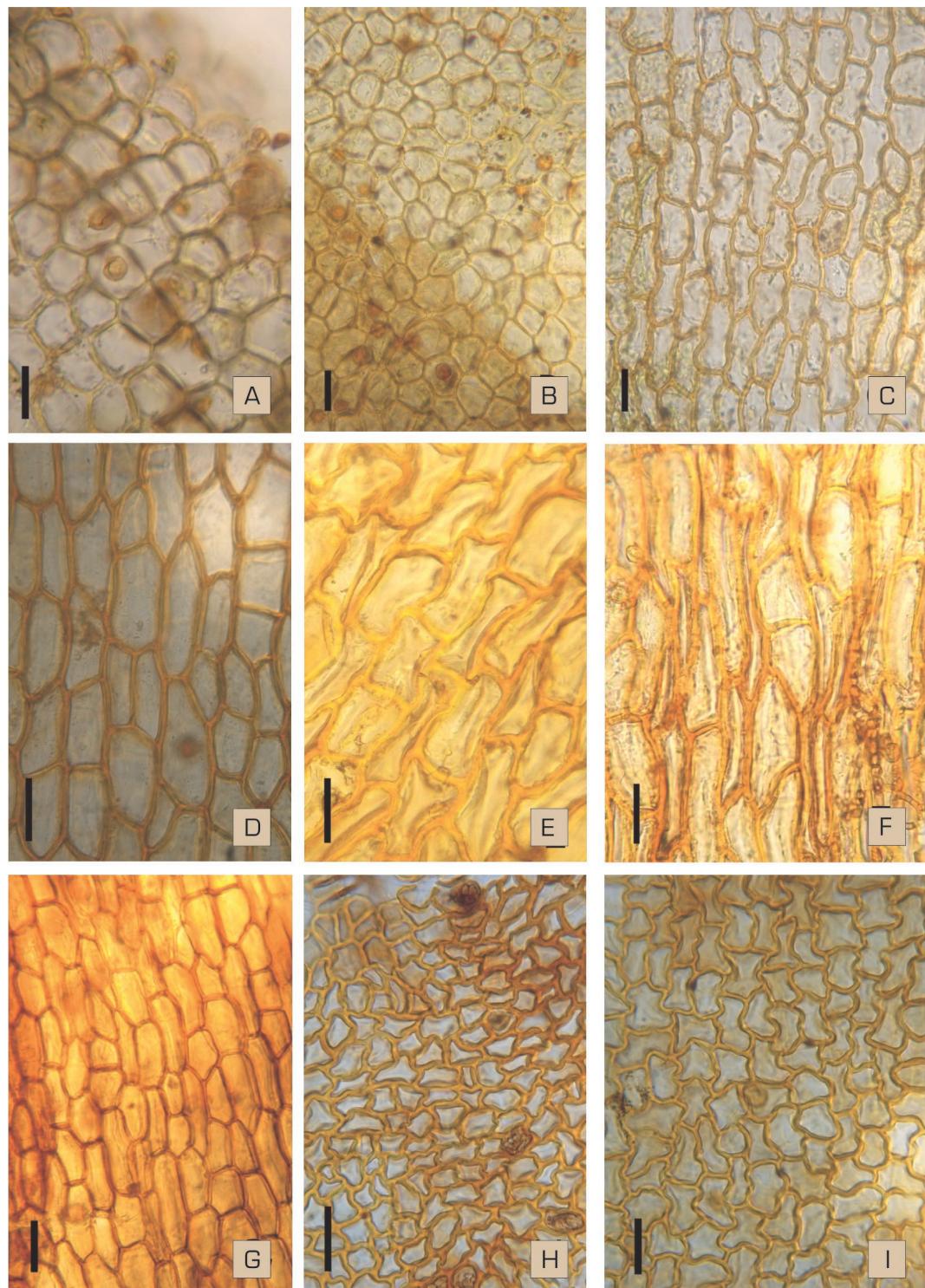


Figure 6. Exothelial cells. A – *P. apolensis*; B – *P. papillosa*; C – *P. pseudobarbula*; D – *P. cruda*; E – *P. lonchochaete*; F – *P. salinaeae*; G – *P. tenuifolia*; H – *P. wahlenbergii*; I – *P. drummondii*. Scale bars = 50 µm.

species they are abundant but when the neck is poorly differentiated, they are scarce (Figure 7). Despite their large size in *P. oerstediana*, they are difficult to see due to the brown color of the guard cells. They are mostly phaneroporous, but cryptoporous in *P. apolensis*, *P. wahlenbergii*, *P. papillosa*, *P. lonchochaete*, and *P. magnifica*. In *P. cruda*, phaneroporous and cryptoporous stomata can be found in the same capsule.

ANNULUS

In the South American species with inclined, cylindrical capsules and a distinct neck, the annulus is formed by more than two rows of vesicular cells. Only in *P. lonchochaete* the annulus is formed by a single row of large vesicular cells that reach 1/3 of the length of the peristome, and in *P. wahlenbergii* is rudimentary or absent. The kind of dehiscence by the annulus is constant within the species. In all polysetous species, the annulus is revolute except in *P. bequaertii*.

PERISTOME

The peristome of *Pohlia* is double, well-developed, and of the «bryoides» type. The only eperistomate species of the genus is the African *P. bequaertii* (Suárez & Schiavone, 2008a). The exostome teeth are lanceolate, gradually acuminate and usually rounded at the apex, except in *P. cruda*, *P. longicollis*, *P. nutans*, and *P. wahlenbergii* that are acute. The teeth are brown, coarsely papillose in the upper third, but gradually become more finely roughened toward the base, trabeculate and bordered, except in *P. apolensis*, *P. papillosa* and *P. pseudobarbula*. They are generally free, except in *P. papillosa* and *P. apolensis*, which have teeth that are fused at their base, a characteristic of the genus *Pseudopohlia*. The endostome varies from hyaline to weakly yellowish, is papillose, has a high basal membrane that reaches half the height of the endostome or longer. The endostome segments are keeled and perforate, except in *P. elongata* and *P. longicollis*, where they are almost entire. The cilia are long and nodose in *P. cruda*, *P. longicollis*, *P.*

nutans, *P. oerstediana*, *P. wahlenbergii*, *P. lonchochaete*, and *P. magnifica*; but short and rudimentary in *P. chilensis*, *P. tenuifolia*, *P. elongata* and *P. wilsonii*. *P. salaminae* can have both types of cilia, whereas cilia are absent in *P. apolensis*, *P. drummondii*, *P. papillosa* and *P. pseudobarbula*.

TAXONOMIC TREATMENT

KEYS TO PROPAGULIFEROUS *POHLIA* IN LATIN AMERICA (STERILE PLANTS)

- 1 Plants with abundant, reddish-brown rhizoidal propagula going from ellipsoidal to rounded, without axillary propagula *P. wilsonii*
- 1' Plants without rhizoidal propagula, with axillary propagula 2
- 2 Costa ranging from percurrent to short excurrent; propagula without leaf primordia *P. lonchochaete*
- 2' Costa percurrent; propagula with leaf primordia 3
- 3 Propagula single in the axils of leaves, with coloured laminate leaf primordia differentiated from the body of the propagulum *P. drummondii*
- 3' Propagula numerous in the axils of leaves, laminate leaf primordia and body of propagula of the same color 4
- 4 Leaf primordia large, apical to subapical *P. pseudobarbula*
- 4' Leaf primordia small, always apical 5
- 5 Propagula elongate, oblong, obconic or linear-vermicular *P. papillosa*
- 5' Propagula rounded to short-oblong 6
- 6 Propagula red to orange, leaf primordia 1–4 with uncinate apex *P. apolensis*
- 6' Propagula yellowish brown, leaf primordia 4–9 with erect apex *P. australis*

KEYS TO PROPAGULIFEROUS *POHLIA* IN LATIN AMERICA (FERTILE PLANTS)

- 1 Exostome teeth fused near the base, not trabeculate, not bordered 2
- 1' Exostome teeth free, trabeculate, bordered 4
- 2 Exothelial cells smooth *P. pseudobarbula*
- 2' Exothelial cells bulging 3
- 3 Propagula green, yellow or pink, linear-vermicular,

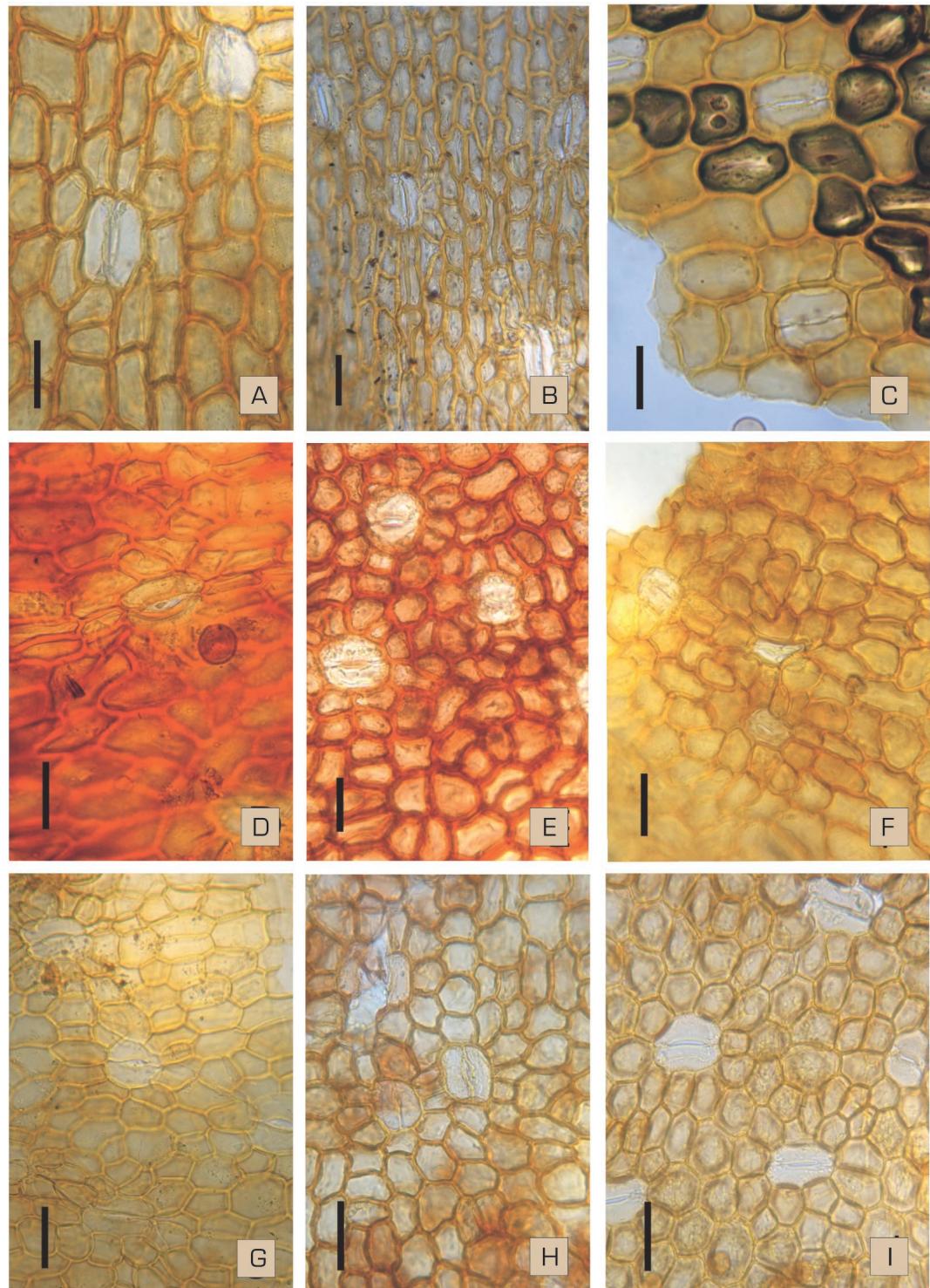


Figure 7. Stomas: A – *P. cruda*; B – *P. elongata*; C – *P. nutans*; D – *P. oerstediana*; E – *P. magnifica*; F – *P. ionchochaete*; G – *P. tenuifolia*; H – *P. drummondii*; I – *P. papillosa*. Scale bars = 50 µm.

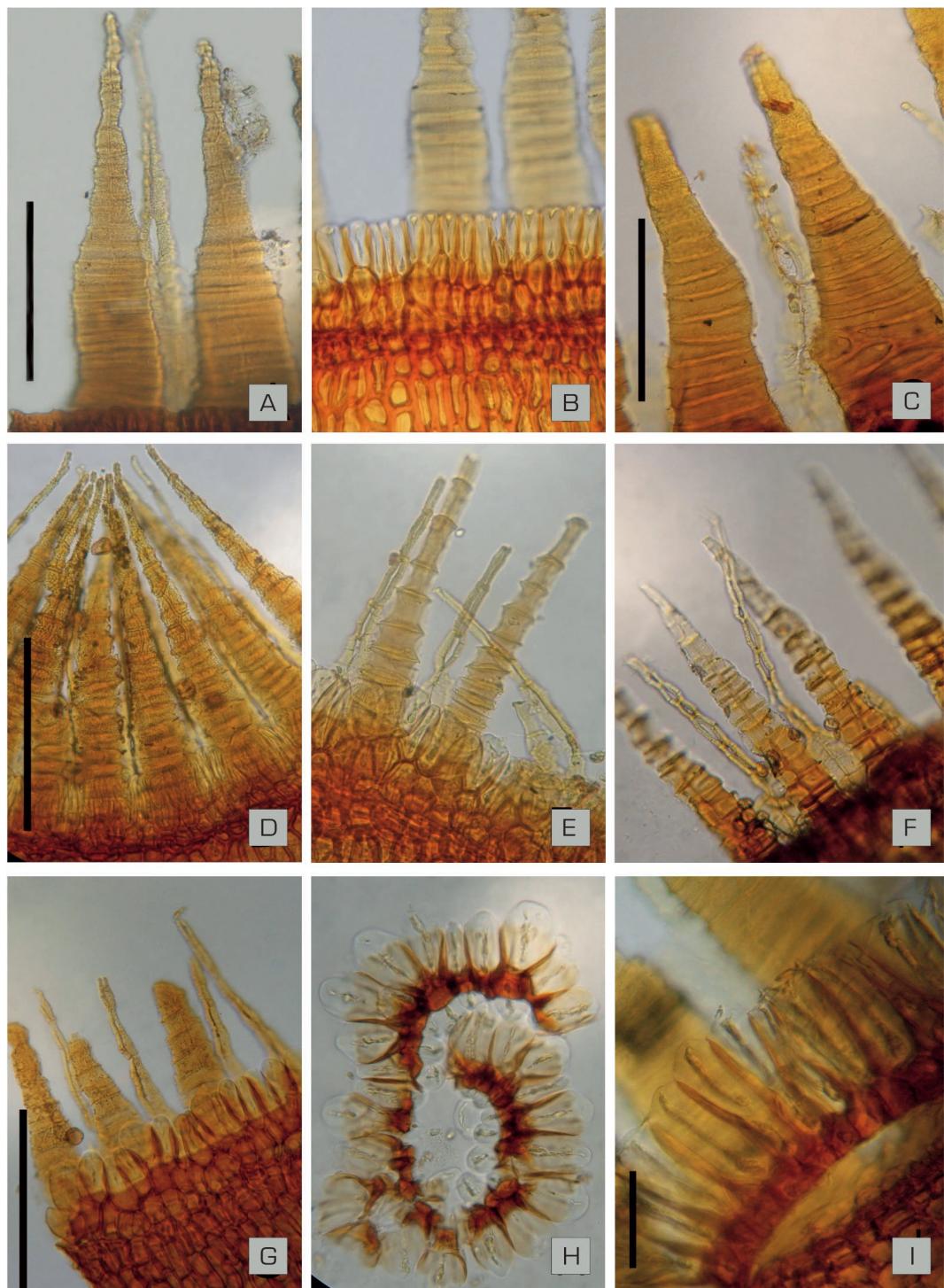


Figure 8. *P. elongata*: A – Peristome, B – Annulus; *P. oerstediana*: C – Peristome; *P. tenuifolia*: D, E – Peristome and annulus; *P. salaminae*: F – Peristome; *P. chilensis*: G – Peristome, H – Annulus; *P. ionchochaete*: I – Annulus. Scale bars: A, B = 50 µm; C, G = 150 µm; D, E = 170 µm; I = 90 µm.

- 3' rarely oblong, leaf primordia erect *P. papillosa*
- 3' Propagula red, rounded, ovoid to obovoid, leaf primordia uncinate *P. apolensis*
- 4 Perichaetal leaves well differentiated from vegetative leaves; neck longer than urn *P. wilsonii*
- 4' Perichaetal leaves poorly differentiated from vegetative leaves; neck shorter than urn 5
- 5 Plants dioicous; exothecial cells with flexuose, collenchymatous walls; leaf primordia well differentiated *P. drummondii*
- 5' Plants synoicous; exothecial cells slightly flexuose; leaf primordia absent *P. lonchachaete*

Pohlia apolensis R.S. Williams, Bull. New York Bot. Gard. 6 (21): 229. 1909.

Type: BOLIVIA. APOLO: 1730 meters elevation, on sandy soil, 19 Feb 1902, *Williams 1882* (Lectotype designated here: NY!, isotypes: BM!, H!, JE!) (Figures 2(F), 4(C), 6(A), 9, 10)

Pohlia richardsii A.J. Shaw, Contr. Univ. Michigan Herb. 15: 253 f. 16. 1982.

Type: COSTA RICA. ALAJUELA: Volcán Poás, ca. 2500 m, *R. Richards 6010* (Holotype: MICH!), *syn. nov.*

Plants small, green to yellow-green, forming mixed turfs. Stems 5–15 mm long, reddish, branched by 1–4 innovations; in cross section rounded with central strand well developed. Axillary hairs 30–50 μm long, with 1–2 basal brown cells and 2–3 distal hyaline cells. Leaves flexuose when dry, spreading when wet, 0.8–1.2 \times 0.2–0.7 mm, lanceolate; apex acute; margins flat to weakly recurved, serrate towards the apex; costa robust, ending 4–5 cells before the apex, deep red at the base; laminal cells thin-walled, the apical ones short to long rhomboidal, 40–60 \times 6–9 μm ; median cells long rhomboidal to fusiform, 85–100 \times 8–12 μm ; basal cells short-rectangular, 35–60 \times 12–15 μm . Propagula numerous, clustered in leaf axils, 80–160 μm , red or orange, spherical, ovoid to obovoid, with 1–4 uncinate apical leaf primordia. Dioicous. Perigonia and perichaetia terminal; perichaetal leaves longer than vegetative ones, 2.2 mm long. Setae 1 per perichaetium, 10–23

mm long, straight, reddish; capsules inclined, broad-pyriform, 2.0–3.5 mm long, with well-developed neck, shorter than the urn; exothecial cells isodiametric to short-rectangular, straight-walled, bulging, 35–55 \times 18–40 μm ; stomata phaneroporous to slightly cryptoporous; annulus of 1–2 rows of vesicular cells, irregular; exostome teeth yellowish-white to white, 250–300 μm long, blunt at the apex, not bordered, trabeculate, papillose; endostome white hyaline, 260–265 μm long, basal membrane short, segments papillose, flat, entire, cilia absent; opercula conic, apiculate. Spores 11–16 μm in diameter, finely papillose.

SPECIMENS STUDIED

NORTH AMERICA. MEXICO. MICHOACÁN: San Juan Nuevo, Patzingo, 19°28'N, 102°11'W, 2400 m, on soil, along road in rather open montane Pine-Oak-forest, 03–06 Oct 2004, *M. Burghart 4505* (MO, NY), 4457 (MO). CENTRAL AMERICA. COSTA RICA. ALAJUELA: Vicinity of crater of volcán Poás, along trail from parking area to Lagoon, Eriaceous shrub vegetation, 32 km NW of N of city center of San José, 2500 m, 10°11'N, 84°14'W, 24 Mar 1973, on ground, *M. & C. Crosby 6280, 6277* (MO, CR), Bosque pluvial montano bajo, 2300–2700 m, talud húmedo, suelo mineral, Aug 1973, *D. Griffin III et al. 019973* (NY); SAN JOSÉ. Cerro de La Muerte, ca 3 m, NW Villa Mills, 3000 m, 29 Aug 1968, on earth bank along road, *R. Koch 5099* (MO, NY), Premontane rainforest, Tapantí Reserve, 1400–1700 m, Cartago, 07 Dec 1982, *L. Gomez #19381* (MO). DOMINICAN REPUBLIC. INDEPENDENCIA: 4 km S of El Aguacate on road to Pedernales, 18°19'N, 71°42'W, moist forest, 21 Mar 1981, *W. Buck 4707* (NY); LA VEGA: Arroyo Los Flacos, 0.5 km S of pyramids, 14 km S of Valle Nuevo, small stream and ravine, 7400 ft., 15 May 1982, *W. Buck 8634* (NY); SAN JUAN: Pico Duarte and adjacent highlands, 3000–3150 m, rock outcrops and open pine cloud forest, 19°01'N, 71°00'W, 15 Jan 1987, *W. Buck 14278* (NY), The Pyramids, 40 km S of Constanza on road to San José de Ochoa, 7600 ft., pine-tussock grass vegetation around humid ravine, 18°45'N,

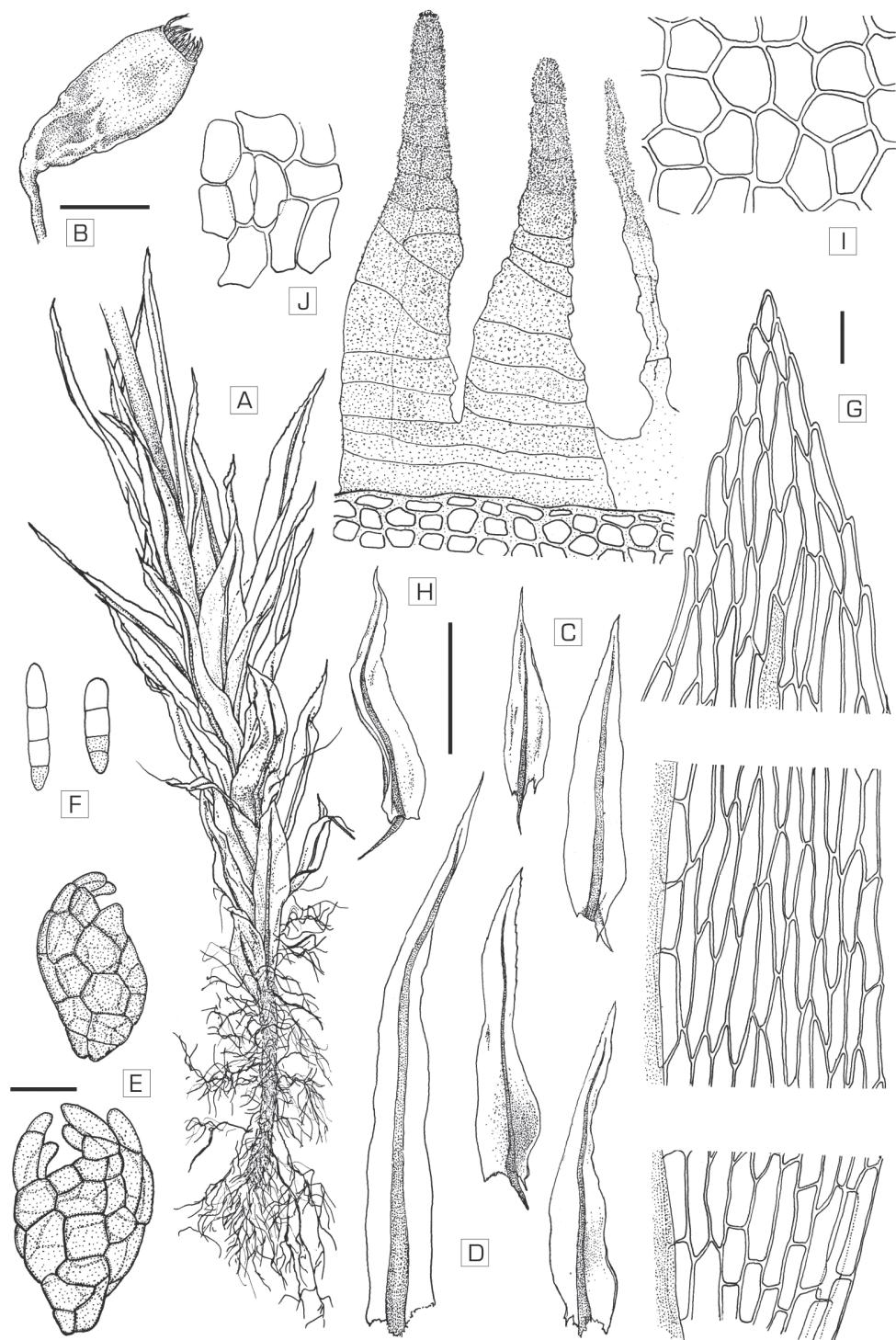


Figure 9. *Pohlia apolensis*. A – Habit in wet, B – Sporophyte, C – Leaves, D – Perichaetial leaves, E – Propagula, F – Axillary hairs, G – Apical, median and basal cells, H – Peristome, I – Exothecial cells, J – Stoma. Scale bars: A, B = 1 mm; C, D = 0.5 mm; E-J= 25 µm.



Figure 10. *Pohlia apolensis*. Propagula. Scale bars = 40 μm .

70°37'W, 10 Jan 1987, W. Buck 14053 (NY).
 SOUTH AMERICA. BOLIVIA. COCHABAMBA: Carrasco, Serranía Siberia, 17°45'S, 64°48'W, 2740 m, 21 May 2003, S. Churchill, M. Decker & F. Mogro 22583 (BOLV, MO), Waldguenze über Tablas, 3400 m, May 1911, T. Herzog 2911 (JE). COLOMBIA. BOYACÁ: Sierra Nevada de Cocuy, Valle de las Playas, overhung stream bank, 4100 m, 8 Aug 1957, P. Grubb & D. Guymer B232 (BM), amongst *Anthoceros* on partially overhung rocky bank to path through secondary forest near Bogotá, 2100 m, 22 Aug 1957, P. Grubb & D. Guymer B365a (BM); CALDAS: Vereda La Corrala, bosque húmedo, 2440 m, Finca «La Zarza» musgo que crece sobre rocas en lugares húmedos y parcialmente sombreados, 19 Jul 1985, L. Albert 5413 (NY); QUINDÍO: Cerca de La Línea, entre Armenia a Ibagué, bosque montano alto, 4°28'N, 75°33'W, 3140 m, sobre tronco con *Prionodon*, 10 Jan 1991, S. Churchill et al. 17224-B (NY). ECUADOR. PICHINCHA: W shore Laguna San Marcos, N slope Volcán Cayambe, in cloud forest, 3450 m, 10 Oct 1984, W. Steere 27590 (MO, NY).

DISTRIBUTION AND HABITAT

Pohlia apolensis is distributed from Central America (Costa Rica, Dominican Republic and Mexico), through the Andean corridor (Bolivia, Colombia and Ecuador) and finds its southernmost limit in Bolivia. It is a frequent species both at volcanic areas near waterways, and in gaps in montane forests from 1700–3700 m. It usually grows associated with *P. papillosa* (its closest relative), which can be easily spotted by its propagular morphology. The axillary microscopic propagula, reddish to orange, with uncinate apex leaf primordia, single *P. apolensis* out from any Neotropical or Southern South American propagiferous species.

NOMENCLATURE

Pohlia apolensis was described by R. Williams (1909), from a single specimen collected in Apolo, Bolivia in 1902. At BM two isotypes of the species could be found. One of them consists of a few fertile plants with few propagula; the other comprises 6

groups of fertile plants with abundant propagula. As the size, color and morphology of propagula define the species, the NY specimen is designated as lectotype. On the other side a detailed examination of the holotype of *Pohlia richardsii* (MICH), a species described by A. J. Shaw (1982), based on a specimen collected by Richards on the Volcán Poás in Costa Rica in 1965, indicates that it is conspecific with *P. apolensis*, so a new synonym is here proposed.

Pohlia australis A.J. Shaw & Fife, New Zealand J. Bot. 23: 183–186. 1985.

Type: NEW ZEALAND. SOUTH ISLAND: Buller Co., Paparoa Mountains, cirque on east flank of Mt. Priestly, 1050–1140 m, 12 Apr 1983, Fife 5487 (CHR not seen) (Figure 11).

Plants medium-sized, green, bright, forming mixed turfs. Stems to 10 mm long, simple, in cross section rounded, with central strand present, poorly developed. Leaves somewhat flexuose in the apex when dry, spreading to erect-spreading when wet, 1.4–2.0 × 0.25–0.35 mm, lanceolate; margins plane, serrate to serrulate in the distal half of the lamina; apex acute; costa robust, percurrent; laminar cells with solid walls, thin, linear-rhomboidal, hexagonal to linear-vermicular, the apical ones 65–90 × 7–12 µm, median cells the same as the apical ones, longer towards the margin, 70–230 × 6–21 µm, basal cells long-rectangular, 40–65 × 10–12 µm. Propagula arising in groups of 3 or more, in the axils of upper leaves, 200–385 µm, yellow, oblong, with 4–9 triangular leaf primordia. Inflorescences and sporophytes unknown.

SPECIMENS STUDIED

CHILE. LOS LAGOS: Reserva Nacional de Llanquihue 50 km SE Puerto Montt, sector Río Blanco, Weg zum Vulkan Calbuco, Lavas Tröme, 41°20'41"S, 72°38'07"W, 1100 m, 21 Mar 2001, W. Frey & F. Schaumann 01-378 (MO) as *P. wahlenbergii*. NEW ZEALAND. WESTLAND LAND DISTRICT: Kelly Range, track to Carroll Hut, k3391–22, 1010 m, mixed subalpine scrub with

Senecio benettii, *Carmichaelia grandiflora*, *Chionochloa flavescens*, *Dracophyllum* sp., etc, 14 mar 1993, A. J. Fife 10066 (CHR).

DISTRIBUTION AND HABITAT

Pohlia australis, a southern species, was considered endemic to the mountainous areas

of New Zealand (Shaw & Fife, 1985), but was recently recorded for South America in southern Chile (Suárez & Schiavone, 2007; Suárez, 2008). The Chilean plants have been collected in the National Reserve Llanquihue, Llanquihue, municipality of Puerto Montt (X Región) where the vascular vegetation is ev-



Figure 11. *Pohlia australis*. A – Habit in wet, B – Leaves, C – Apical, median and basal cells, D – Propagula.

ergreen forest with *Laureliopsis philippiana* (Loosser) Schodde, *Podocarpus nubigenus* Lindl., *Nothofagus dombeyi* (Mirb.) Oerst. and *Luma apiculata* (DC.) Burret, with abundant *Chusquea* sp. in the understory. Despite growing in disjunct areas, the two populations of plants do not differ in morphology. They are generally robust, bright green plants with a strongly serrated leaf apex and large (200–400 µm), yellow, oblong, axillary propagula, with apical leaf primordia. Its propagular morphology differs from that of *P. drummondii* in that its leaf primordia is spread throughout the body and from that of *P. lonchochaete* because of its flattened triangular propagula without leaf primordia. It also differs from other propaguliferous species of New Zealand; actually, *P. ochii* Vitt has long vermicular propagula and *P. camptotrichela* (Renauld & Cardot) Broth. has 150 µm orange propagula.

Pohlia drummondii (Müll. Hal.) A.L. Andrews, Moss Fl. N. Amer. 2: 196. 1935.
≡ *Bryum drummondii* Müll. Hal., Bot. Zeitung (Berlin) 20: 328. 1862. Type: Drummond, Musci Americ. (Rocky Mtns.) no 263 (Lectotype: BM!). Isolectotype: NY!. (Figure 2(E), 4(B), 6(I), 7(H), 12)

Bryum catenulatum Schimp., Syn. Musc. Eur. (ed. 2) 471. 1876. Type: Ben Lomond, J. Stirton (Lectotype: BM!).

Pohlia commutata (Schimp.) Lindb., Musci Scand. 17. 1879. ≡ *Webera commutata* Schimp., Syn. Musc. Eur. (ed. 2) 403. 1876. (Lectotype: BM!).

Pohlia lindbergii Warnst., Beih. Bot. Centralbl. 16: 240. 1904. Type: SCHWEDEN. Darlarna Avesta, Lindnäs, Aug 1881, C. In-debelon (Lectotype: H!).

Plants medium-sized to robust, yellowish green, bright, forming dense, pure turfs. Stems 3–15 mm long, transparent red, simple, in cross section rounded, with central strand well developed. Axillary hairs 50–60 µm long, with 3–4 basal brown cells and 2 distal hyaline cells. Leaves equally distributed along stem, crispatate when dry, spreading when wet, 0.8–1.5 × 0.30–0.50 mm, lan-

ceolate to ovate-lanceolate; apex acute; margins recurved, serrulate towards the apex; costa robust, percurrent, red only at the base; laminal cells thin-walled except at the base, apical cells short- to long-rhomoidal, 38–75 × 7–13 µm, median cells long-rectangular, rhomboidal or fusiform, 30–95 × 7–13 µm, basal cells short-rectangular, 25–50 × 13–20 µm. Propagula usually present in sterile plants, 1 in leaf axils, 500–600 (–1500) µm long, orange, ovate to oblong with well-developed leaf primordia distributed over the body of the propagula. Dioicous. Perigonia and perichaetia terminal; perichaetal leaves slightly differentiated from vegetative ones. Setae 1 per perichaetium, reddish, 1–2.5 mm long; capsules inclined, ovate-pyriform, 2–3 mm long, neck undifferentiated; exothelial cells isodiametric, walls flexuose, 10–35 × 5–40 µm; stomata phaneroporous; annulus of 1–2 rows of vesicular cells; exostome teeth yellow to yellowish-brown, 300–310 µm long, bordered, very trabeculate, most densely papillose near the apex; endostome hyaline, 270–300 µm long, basal membrane high, segments perforate, cilia absent. Operculum conical. Spores 15–20 µm in diameter, papillose.

SPECIMENS STUDIED

NORTH AMERICA. CANADA. BRITISH COLUMBIA: wet bank, Glacier, 21–24 Jul 1941, A. Andrews 459, 17970, 18527 (MO), Lake of Hanging Glaciers, Wilmer Dist., 29 Jul 1928, F. Macfadden 16940 (MO), earth in meadow, Upper Simpson Pass, 7000 ft., 24 Aug 1913, A. Brinkman 9948 (MO), Whistler Mt. Slopes, moraine and outwash area, 6000 ft., 19 Sep 1971, W. Schofield & D. Jamieson 47199 (MO), New Denver: Silverton water hole, on clay banks, 03 May 1926, F. Macfadden 599 (MO), on clay banks, Silverton water hole, New Denver, 03 May 1926, F. Macfadden 599 (MO), small stream bank, glacier, 24 Jul 1941, R. Andrews 459, 18527 (MO). USA. ARIZONA: White House Canyon, Santa Rita Mountains, Santa Cruz County, submerged rivers in stream, 6500 ft., 20 Feb 1924, E. Bartram 132 (MO); CALIFORNIA: Los Angeles, wet

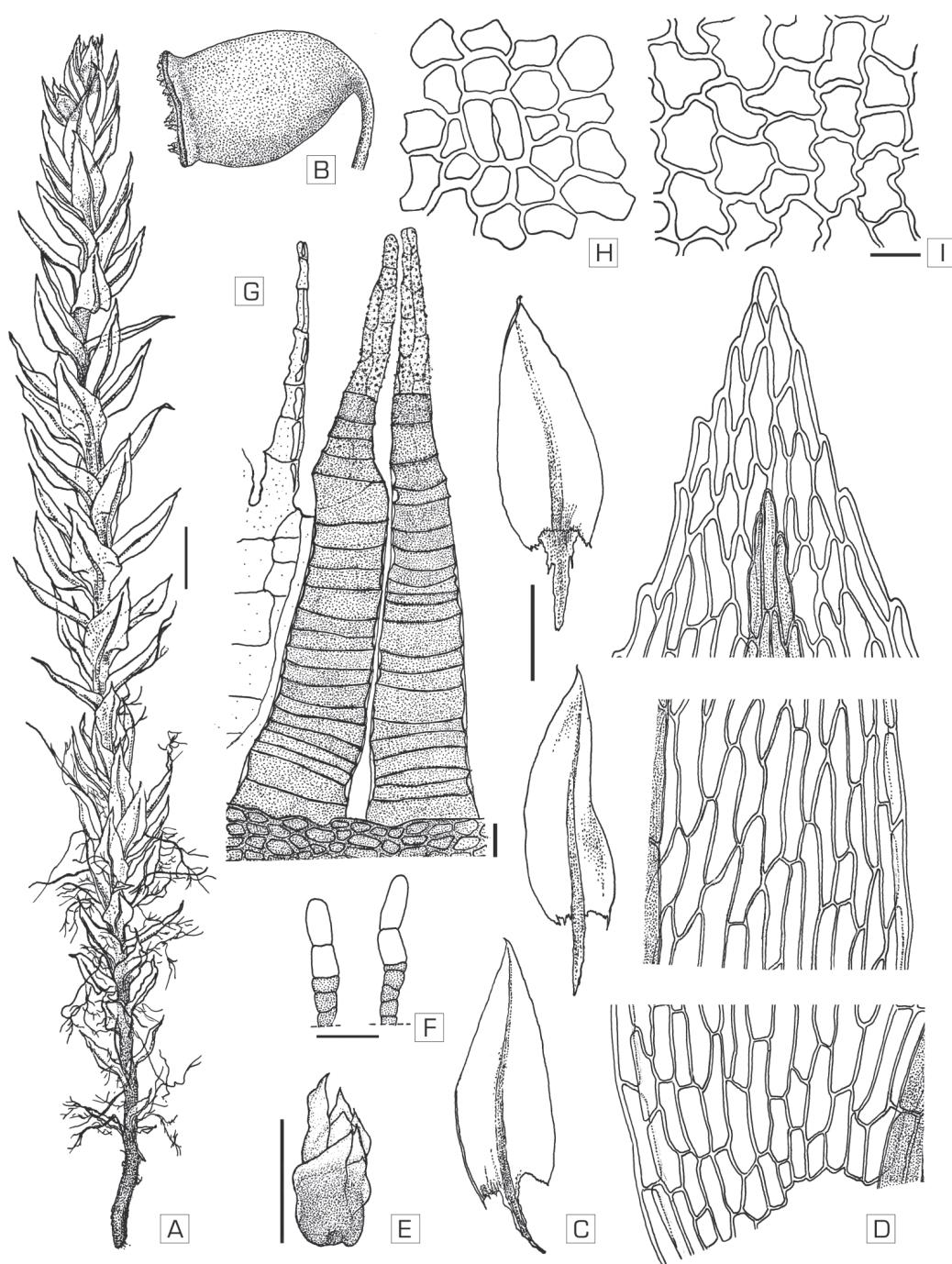


Figure 12. *Pohlia drummondii*. A – Habit in wet, B – Sporophyte, C – Leaves, D – Apical, median and basal cells, E – Propagula, F – Axillary hairs, G – Peristome, H – Stoma, I – Exothecial cells. Scale bars: A, B = 1 mm; C = 0.25 mm; E = 0.5 mm; D, F-I= 25 μ m.

bank, 21 Jul 1941, F. Macfadden 17970 (MO), Alaska, 19 Jul 1976, Wallace s/n (MO); IDAHO: small creek on road to Lucky Boy Mine, Custer Distr., Custer Co., 08 Aug 1941, F. Macfadden #18531 (MO), Custen dist., Adair cruk, alpine stream bank, 8000 ft., 07 Aug 1941, F. Macfadden 18550 (MO); MONTANA: near Columbia Falls, 7000 ft., 04 Sep 1896, R. Williams 341 (MO), 15 Aug 1897, R. Williams 20398 (MO); WHASHINGTON: Goat Mts., near Mt. Rainier, bank of rivulets, 5000 ft., 07 Jul 1898, J. Allen 55 (MO); WYOMING: Park Co., Beartooth Plateau, Cooke City to Red Lodge Highway, west side Beartooth pass, under late snow patch on steep slope north of switchback, rills and snowbeds, 3200 m, 18 Aug 1973, W. Weber b-44318 (MO).

SOUTH AMERICA. ARGENTINA. Nordteil vom National park Los Glaciares: Weg vom Refugio Los Troncos zum Cerro Eléctrico (=ca. 16 km NW El Chalten); ca. 1200 m NN, 49°14'S, 73°5'W, subalpin-alpine Vegetation, auf fench Erde under Felsblock, 20 Feb 2000, F. Müller C1476 (DR), Nordteil vom National Park Los Glaciares: weg vom Campamento Poincenot zum Fitz lookout (= ca. 10 km NW El Chalten); ca. 1100 m NN; 49°18'S, 73°0'W, auf Erde under Steinen sen Gletschersee, 19 Feb 2000, F. Müller C1534, C1493, C1534 (DR). CHILE. Laguna Maule (=ca. 125 km SO von Talca), am Nordufer des Sees, ca. 2500 m NN, Región VII, 36°1'S, 70°30'W, alpine vegetation; auf Erde, 27/28 Mar 1999, F. Müller C223 (DR), Región XII, National park Torres del Paine: Gebirgszug zwischen Campamento Los Perros und Campamento Paso, 600–1100 m NN, 50°56'S, 73°13'W, alpine-subalpine Gebirgsvegetation, 12 Feb 2000, F. Müller C1514 (DR); Región VII, Schutzgebiet Radal 7 Tazas (= 50 km SO Molina): Weg von der Administration (Parque Ingles) ins Valle del Indio, 35°30'S, 70°56'W, 03 Mar 2000, F. Müller C1813 (DR).

DISTRIBUTION AND HABITAT

Pohlia drummondii is widely distributed in the Old World (Austria, Britain, Czech Repuclic, Germany, Finland, Ireland, Norway, Slovakia, France, Switzerland and Po-

land), only in the Iberian Peninsula, it appears as a rare species (Guerra, 2007). In America it shows a remarkable disjunction, having been recorded in the northern regions of Canada and the U.S. and in southern Argentina and Chile. It is usually found in alpine or subalpine habitats in areas near the glaciers. Although the plants studied are fairly uniform, those from the Scandinavian Peninsula are much smaller than the ones in the south of Argentina and Chile. It was found that *Pohlia drummondii* is a species that is rarely fertile. The leaves are crisped with a metallic shine, with a propagulum with indefinite growth in the leaf axills. The propagula are usually solitary, are uniform, 500–600 (-1500) μm long, oblong when young, elongated in the more advanced stages of development, with well-developed laminate leaf primordia, distributed on the body and the apex. Although plants are usually sterile, some fertile plants were also observed, the propagula are absent or very difficult to find, a fact which had already been mentioned by Shaw (1981). These plants can be erroneously associated with other non propaguliferous northern *Pohlia* specimens, such as *P. obtusifolia* (Brid.) L. Koch (*J. Shevock* 26053, MO) and *P. bolanderi* (Sull. & Lesq.) Broth. (*Weber & Wittmann* B-110, 944, topotype MO!). However, they are different in that *P. obtusifolia* plants are pink to reddish, with broad cucullate leaf tips, and *P. bolanderi* are bluish green with erect, somewhat keeled leaves.

Pohlia papillosa (Müll. Hal. ex A. Jaeger) Broth., Nat. Pflanzenfam. I(3): 552. 1903.

\equiv *Brachymenium papillosum* Müll. Hal. ex A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 122. 1875. a» *Bryum papillosum* Müll. Hal., Syn. Musc. Frond. 1: 326. 1848. hom. illeg. – non *B. papillosum* Dicks. 1801. Type: VENEZUELA. CARACAS: Columbia, ad Galipan, 3000 pd., 1845b, F. Schlim 346 (Lectotype: NY!). (Figures 4(A,E,F), 6(B), 13, 14).

Brachymenium tenellum (Schimp.) Schimp., Mém. Soc. Sci. Nat. Cherbourg 16:

195. 1872. \equiv *Bryum tenellum* Schimp., Syn. Musc. Frond. 2: 572. 1851. Type: MEXICO. Pico de Orizaba inter Philonotulas, Liebmamn (Lectotype: BM-Schimp!, isotype: NY!).

Pohlia subglobosa (Schimp. ex Besch.) Broth., Nat. Pflanzenfam. I(3): 552. 1903. \equiv *Brachymenium subglobosum* Schimp. ex Besch., Ann. Sci. Nat., Bot., sér. 6, 3: 204. 1876. Type: ANTILLES. Dans les terrains caillouteux des bords de la riviere Rouge (Guad.), 650 m, 149 (Lectotype: BM-Besch!, isotypes: B!, BM-Hampe!, H!, NY!, PC!).

Pohlia longipedicellata (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 552. 1903. \equiv *Bryum longipedicellatum* Müll. Hal., Linnaea 42: 477. 1879. Type: VENEZUELA, without locality, Fendler 82 (Lectotype here designated: BM!, isotype: PC!, H-Br!, NY!) syn. nov.

Bryum mammulosum Müll. Hal., Bull. Herb. Boissier 5: 550. 1897. \equiv *Webera mammillosa* (Müll. Hal.) Broth., Nat. Pflanzenfam. (ed. 2) 10: 362. 1924.

\equiv *Pohlia mammillosa* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 552. 1903. \equiv *Brachymenium mammulosum* (Müll. Hal.) Paris, Index Bryol. Suppl. 39. 1900. Type: JAMAICA, growing on shady bank near Cinchona, 5,200 ft., 4 Dec 1896, W. Harris 11023 (Lectotype: NY!).

Pohlia verrucosa (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 552. 1903. \equiv *Bryum verrucosum* Müll. Hall., Nuovo Giorn. Bot. Ital., n.s., 4: 22. 1897. Type: BOLIVIA. Provincia Cochabamba prope choquecamata, jun 1889, Germain (Lectotype here designated: H!, isotype: NY!) syn. nov.

Bryum anisodontacum Dusén, Rep. Princeton Univ. Exp. Patagonia, Botany 1896–1899, Botany 8(3): 122. 1903, nom nud. Based on: «CHILE. Chile australis, ad lac. Todos los Santos, in Terra», 1 Jul 1897, P. Dusén 733 (BM!).

Plants small, yellowish-brown, somewhat glossy. Stems 5–25 mm long, yellowish, simple or with 1–2 innovations; in cross section rounded to elliptical, with central strand well developed. Axillary hairs 50–150 μm long, with 1–3 basal brown cells and 1–3

distal hyaline cells. Leaves distant in sterile shoots, comose in the fertile shoots, appressed when dry, spreading to erect when wet, 0.7–1.0 \times 0.1–0.5 mm, linear-lanceolate; apex acute; margins plane, serrulate near the apex; costa robust, subpercurrent, colored at the base; leaf cells lax, thin-walled, apical cells long-rhomoidal to fusiform, 30–85 \times 6–14 μm , median cells long-hexagonal, 45–90 \times 6–12 μm , basal cells short-rectangular, more thick-walled, 28–50 (–61) \times 6–23 μm . Propagula grouped in leaf axils, numerous (rarely one), 70–250 μm long, usually hyaline, linear-vermicular, oblong or obconical, 1–4 apical leaf primordia. Dioicous. Perichaetial leaves oblong-lanceolate, 2.0–3.0 \times 0.3–0.4 mm; apex serrate. Setae 1 (–2) per perichaetium, 14–40 mm long, reddish brown; capsule inclined, pyriform, 1.8–3.0 \times 0.8–1.0 mm, with distinct neck, shorter than urn; exothelial cells with mammillose walls, hexagonal-rectangular, 25–52 \times 12–48 μm ; stomata cryptoporous in the neck; annulus 1 (–2) rows of vesicular cells; exostome teeth yellow, fused at the base, 250–290 μm long, weakly bordered, scarcely trabeculate, strongly papillose; endostome hyaline, papillose, 170–250 μm long, basal membrane short, segments entire or scarcely perforate, cilia absent. Operculum conic, short-rostrate. Spores 11–20 μm in diameter, weakly papillose.

SPECIMENS STUDIED

NORTH AMERICA. MEXICO. CHIAPAS: steep slope with evergreen cloud forest on the NW side of Cerro Tzontehuitz, Municipio de San Cristobal de las Casas, 2830 m, growing on soil, 08 May 1988, D. Bredlove 67323 (MO); HIDALGO: Mineral del Chico, May 1925, C. Orcutt 6641, 6761 (FH); OAXACA: Tehuantepec s/n (MO); forest at km 124 along Hwy. ca. 50 air km S of Tuxtla, 1500–2500 m, on dry bank in deep ravine, 29 Aug 1974, J. & R. Conrad 3229 (MO), cloud forest along Hwy. 175 at km 90, ca. 50 air km S. of Tuxtla, on dirt slope, 2000–3000 m, 29 Aug 1974, J. & R. Conrad 3210 (MO), ravine with running water, 49 miles from Tuxtla going toward Oaxaca

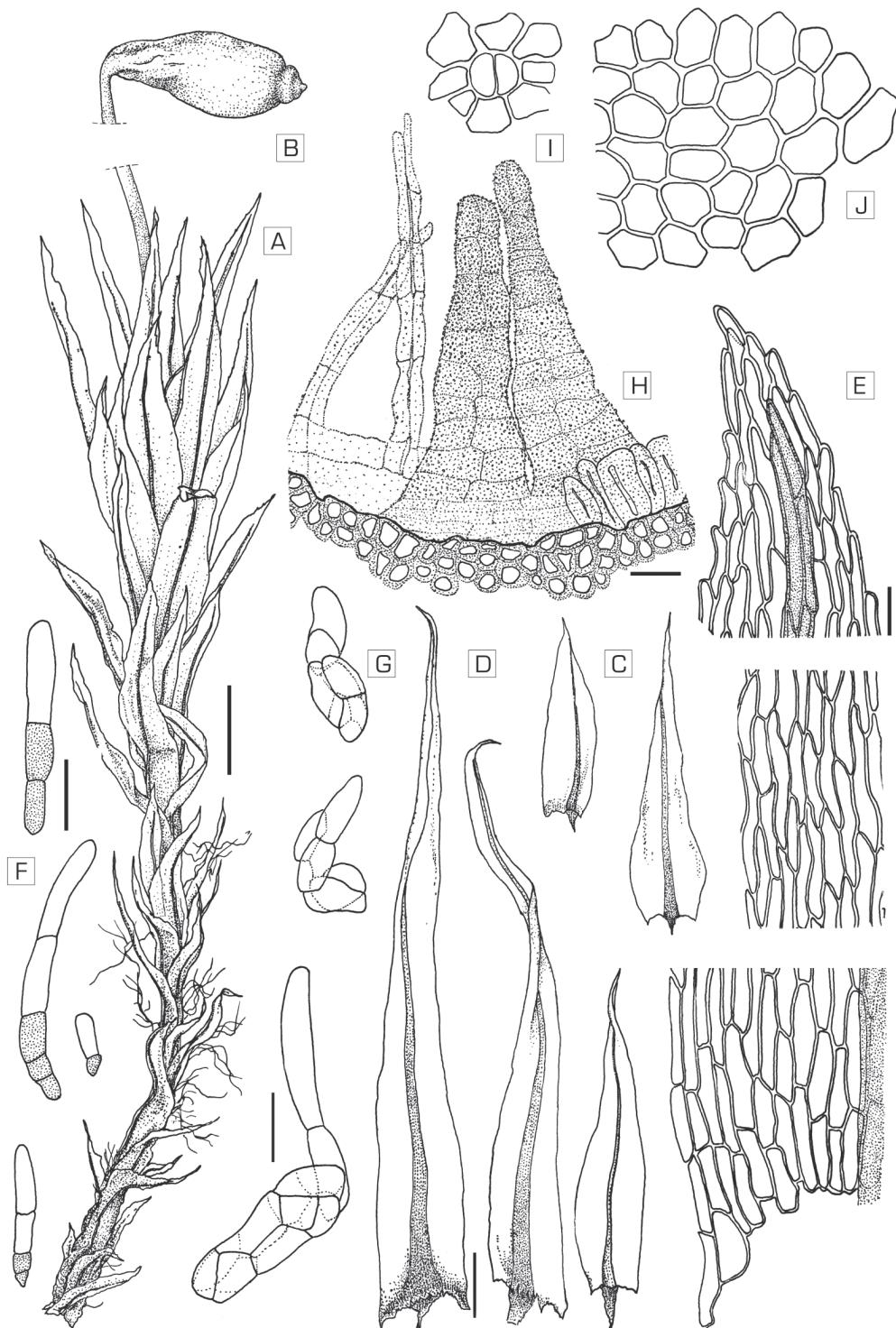


Figure 13. *Pohlia papillosa*. A – Habit in wet, B – Sporophyte, C – Leaves, D – Perichaetial leaves, E – Apical, median and basal cells, F – Axillary hairs, G – Propagula, H – Peristome, I – Stoma, J – Exothecial cells. Scale bars: A, B = 1 mm; C, D = 0.25 mm; E-J= 25 μ m.

on Highway 175, slope north, 6300 ft., 26 Dec 1970, on soil under rock, *G. Manuel 719* (MO), on banks of earth near Tezuitlan, 27 Oct 1908, *C. Pringle* (FH); PUEBLA: on bank of earth near Tezuitlan, 27 Oct 1908, *Det: Cardot* (FH), Tezuitlan, 08 Sep 1910, *C. Orcutt 4059* (FH). CENTRAL AMERICA. GUATEMALA. BAJA VERAPAZ: near Gícaro, 4800 ft., roadside bank, 21 Feb 1945, *A. Sharp 2673* (FH); DE SOLALÁ: sandy clay bank along road to Quezaltenango, ca. 18 miles W, 06 Feb 1975, *F. Hermann 26337* (B) as *P. proligera*; HUEHUETENANGO: about Laguna de Ocubilá, east of Huehuetenango, 1900 m, wet bank, 07 Jan 1941, *P. Standley 82705* (FH), moist bank of trail, between Soloma and San Juan Oxcoy, 7300 ft., 04 Jan 1946, *A. Sharp 4974* (FH), Cerro above Tecpam, moist shaded bank, 9300 ft., 15 Feb 1945, *A. Sharp 2580* (FH); QUEZALTENANGO: Vicinity of Fuentes Georginas, slopes of Volcán de Zunil, 2300–2500 m, 03 Feb 1941, *P. Stanley 85986, 86025* (FH), Región de las Nubes, South San Martín Chile Verde, 2250 m, 16 Jan 1941, *P. Standley 83645* (FH), Aguas Amargas, on the western slope of Volcán de Zunil, 2450 m, 14 Jan 1941, *P. Standley 83308* (FH); SAN MARCOS: along road between San Sebastián at 21 km and 8–18 miles northwest of San Marcos, 2700–3800 m, 15 Feb 1940, *J. Steyermark 35631* (FH), Puente de Nahuatl-aa, near San Marcos, 2280 m, 22 Feb 1939, *P. Standley 66268* (FH); SUCHITEPÉQUEZ, southern lower slopes of Volcán Zunil, near Finca Las Nubes, east of Pueblo Nuevo, 1000 m, 01 Feb 1940, *J. Steyermark 35362* (FH); TOTONICAPÁN: open slopes on Sierra Madre Mountains, South of Totonicapán, near Mirador (Km ± 170), 2800 m, 20 Dec 1972, *L. Williams, A. Molina & T. Williams 41450B* (MO). HAITI. Jardín Boís, mormesdes comunissaires, 1600 m, road bank, 03 Jan 1946, *L. Holdridge 1219, 3177* (FH). PANAMA. BOCAS DEL TORO: región of Cerro Colorado on trail along a quebrada c. 7.5 miles from chami camp. C., 8°35'N, 81°45'W, forest, 1220–1250 m, on old road-cut, 13 Apr 1986, *G. McPherson 8883c* (MO), Cerro Colorado, 4.3 mi above Chami Camp, roadside

along the ridge, ca. 3 mi, 8°35'N, 81°45'W, 1700 m, on mud at edge of road, 21 Jun 1986, *B. Allen 5304, 5325, 5343* (MO); CHIRIQUÍ: east of Boquete along steep, forested slopes and wooded pastures on Cerro Azul near Quebrada Jaramillo, 1620–1700 m, 11 Aug 1974, *T. Croat 26888* (MO). JAMAICA. Blue Mts., *Hitchcock 1893* (MO); ibidem. 6000 ft., plants scattered, 12 Jul 1932, *P. Patterson 56* (FH); ibidem. terrestrial, montane rain forest, 21 Jan 1951, *R. Robbins 37, 40* (FH); ST. THOMAS: trail to Blue Mountain Peak, between Peak and Portland Gap, 5500–7300 ft., 76°36'W, 18°03'N, on moist trailside bank, 24 Jul 1963, *M. Crosby 1357* (MO); ST. ANDREW: vicinity of St. Helens, 475 m, Mar 1920, *W. Maxon & E. Killip 644* (FH), Trail from St. Helens Gap to Latimer River, 1400–1475 m, 9 Mar 1920, *W. Maxon & E. Killip 894* (FH). COSTA RICA. SAN JOSÉ: La Palma area, crest of ridge, on regional road 220 beyond San Jerónimo, 1640 m, 10°03'N, 83°59'W, 23 Mar 1973, *M. & C. Crosby 6262a* (MO); CARTAGO: Montane forest ca. 5 km, northeast of Orosi, 4500 ft., 17 Aug 1991, *R. King C91-62* (MO), I.C.E. Tapanti project area, W bank of Río Grande de Orosí, above confluence with Río Villegas, 25 km SE of city center of Cartago, 1640 m, 9.41°N, 83.46°W, 25 Mar 1973, on sunny bank, *M. & C. Crosby 5927* (MO), paramos lluviosos del Cerro de la Muerte, montaña alta pluvial, 27 Oct 1969, *L. Gómez 2111* (MO), 6.2 miles from San Rafael de Heredia on Volcán Barba, swampy, moss cloud forest, *Clusia*, small palms, *Cyclanthus*, 6400 feet, 30 Jul 1967, *F. Bowers 244d* (MO); PUNTARENAS: Coto Bus Canton, faja costeña de Puntarenas, frente al cerro Paraguas, fila de cruces, San Vito, 8°57'N, 83°04'W, 1400 m, 08 Jun 1995, *G. Dauphin 1775* (MO); ALAJUELA: just above Poasito on road to Volcán Poás, stream gully, 30 km NW of N of city center of San José, 2000 m, 10°10'N, 84°13'W, 24 Mar 1973, on shaded vertical bank, *M. & C. Crosby 6305* (MO). EL SALVADOR. Meadow along trail to Guatemala from Hacienda Monte Cristo area, on rock, 30 Oct 1977, *M. Watson Es-0107* (MO), Trail behind hacienda

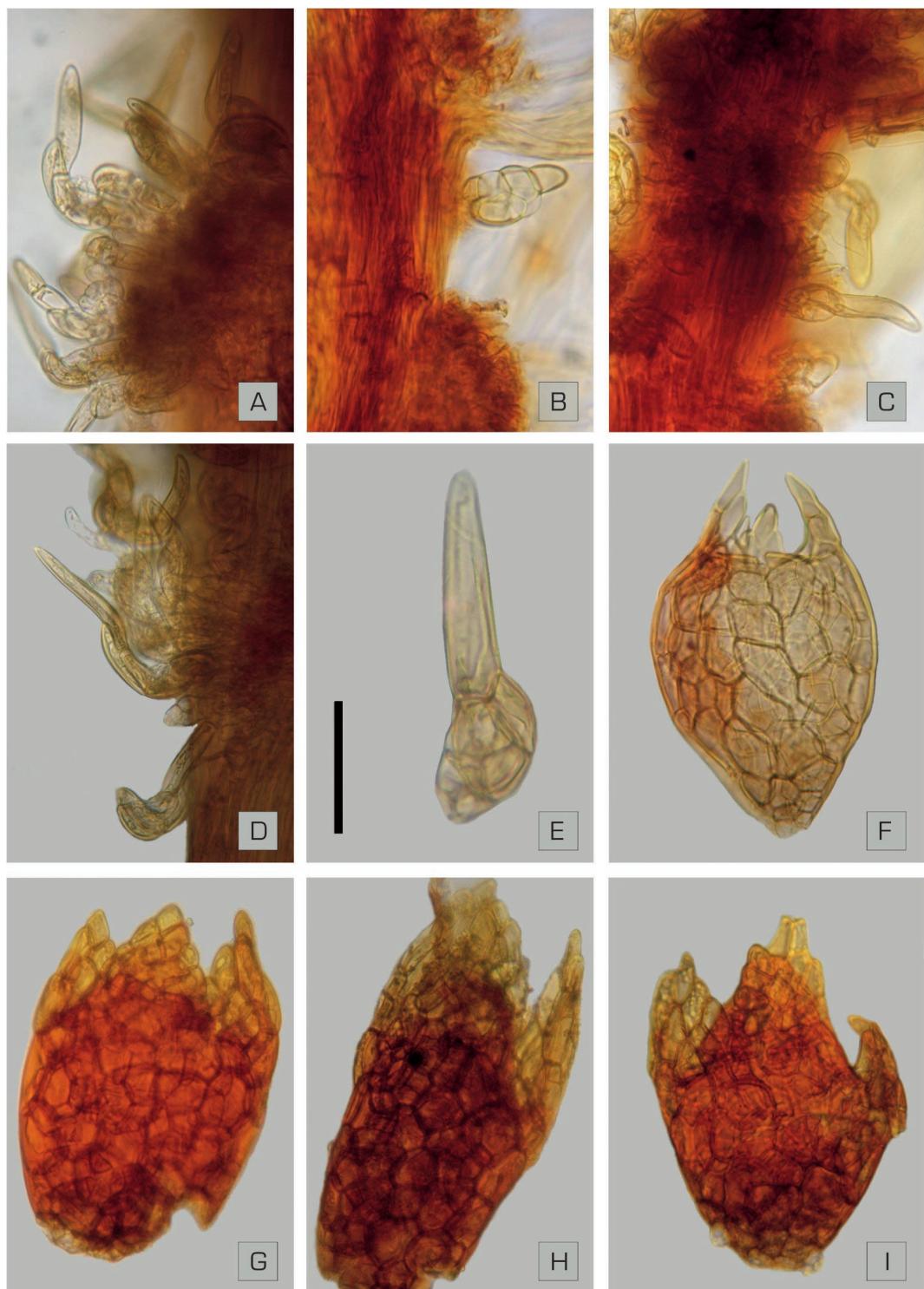


Figure 14. *Pohlia papillosa*. Propagula. Scale bars = 20 μm .

da Monte Cristo which breaks off from the summit trail, this is a wide trail cut through soil banks 3 m high in places, lower portion of earth mound, 26 Oct 1977, M. Watson ES-0042 (MO); SAN VICENTE: Volcán de San Vicente, 19 Feb 1962, E. Moltaalvo M1 (MO). DOMINICAN REPUBLIC. Cordillera Central, Prov. La Vega, donde le camino entre los poblados rurales de paso bajito y La Sal cruce el río Jimenoa, 19°04'N, 70°35'W, 850 m, 14 Apr 1982, T. Zanoni, M. Mejía & J. Pimentel 20104 (MO), Constanza, El Montazo, sobre ladera húmeda, 1500 m, 19 Jan 1975, Alaia & Lieger 22300 (FH). HONDURAS. Cusuco National Park, from Río, Cusuco to summit of Cerro Cantiles, ca. 22 km W of San Pedro Sula, 16 km S of Cuyamel, 15°31'N, 88°39'W, 1400 m, 1600–2000 m, on sand bank along trail, 19 Mar 1993, B. Allen 14239 (MO); Montaña de Celaque, along Río Arquegual 7,5 km SW of Gracias, 14°34'N, 88°39'W, 1400 m, at base of boulder by stream, 11 Nov 1991, B. Allen 11100 (MO).

SOUTH AMERICA. ARGENTINA. TUCUMÁN: Depto. Chicligasta, Estancia El Portezuelo, 1900 m, 19 Jan 1947, Digilio-Grassi 1290 (FH). BOLIVIA. INCACORRAL: Paracti, 2000 m, 06 1911, T. Herzog 5003 (B); SANTA CRUZ: Manuel M. Caballero, 15 km E de Siberia por camarapa, bosque montano nublado de Serranías de Siberia, muy húmedo, mucho viento, musgo sobre suelo rocoso, al lado de la quebrada, entre el bosque y potrero, 17°49'S, 64°40'W, 2500 m, 09 Sep 2002, S. Churchill 21974 (MO), Florida, Municipio Mairana, 23 km nordeste de Mairana, Bosque nublado secundario con arbustos, poco helecho arbóreo, 18°03'S, 63°54'W, 2100–2300 m, 30 Mar 2002, S. Churchill et al 21425a (MO). COLOMBIA. EL CAUCA: 3100–3300 m, 11 Jun 1922, Pen nell 6649 (MO, FH); NARIÑO: Pasto Municipio, La Cuchilla-El frailejona, 8 km SE de Mocondino, 3050–3360 m, 11 Dec 1993, B. Ramírez 5988 (MO), Municipio de Pasto, corregimiento de Santa Bárbara, Río Bobo-Santa Barbara, 1°5'N, 77°18'W, 3000 m, 21 Jan 1995, B. Ramírez 6718 (MO), Pasto Municipio, Bosque de Danza, con Cerat-

odon, 1°10'N, 77°16'W, 2700–2830 m, 28 Mar 1995, B. Ramírez 7016 (MO); MAGDALENA: Municipio de Santa Marta, Vereda La Tagua, Sito Filo Cartagena, bosque premontano, 10°5'N, 74°03'W, 900–1545 m, 19 Jul 1992, S. Churchill & E. Linares 18399 (MO), Sierra Nevada de Santa Marta, Hacienda Cucinati, 1250–1500 m, 08 Aug 1935, G. Martini 3201 (FH); ANTIOQUIA: Municipio de Jardín, 8–10 km, 05°32'N, 75°44'W, 2900 m, en ventanas, bosque montano húmedo, sobre talud con Pilopogon, 04 Oct 1987, S. Churchill & O. Marulanda 15741 (MO, HUA), Paramos de Chipaque above Bogotá, 25 Feb 1951, R. Schultes 11401 (MO), Municipio de Duitama, páramo «La Rusia», páramo with stream and Polylepis, 3550 m, on side of boulder, 26 Oct 1988, R. Ireland 23686 (MO); CALDAS: Municipio de Villa María, Carretera Manizales-Bogotá, sobre la carretera que conduce al Nevado del Ruiz, 4°55'N, 75°21'O, 3480–3500 m, páramo y bosque ceja, 11 Apr 1990, S. Churchill et al. 16263-b (HUA); HUILA: Comisaria del Caqueta, Cordillera Oriental sobre el filo divisorio, en Gabinete, 2300–2450 m, 27 Mar 1940, J. Cuatrecasas 8790 (FH); SANTANDER: vicinity of California, 3000 m, dry bank, open hillside, 11–27 Jan 1927, E. Killip & A. Smith 16950 (FH). PERU. CAJAMARCA: Celendrín between Celendrín and Balsas, west of the passes, 06°51'S, 78°05'W, 30 Aug 1973, P. & E. Hegewald 6647 (MO); HUANUCO: Loc. Carpish, ceja de la selva, 1946, L. Holdridge 1219, 3177 (FH), 2600 m, 13 Aug 1977, E. Cerrate 6670 (MO); CARCHI: road Julio Andrade-Palestina, scrub forest, 77°40'W, 0°38'N, 3300 m, 27 Dec 1980, L. Nielsen, J. Jaramillo & F. Coello 29631 (MO, B); CAUCA: Muila, bei Santa Leticia, 06 Jun 1980, B. Hegewald 9873 (MO); LA LIBERTAD: Prov. Huamachuco, ort. La Cabaña (am Río Agu Casa) zn. Huamachuco u. Cajabamba. Erde, 3000 m, 22 May 1973, E. Hegewald (MO); HUAUCE: above rocks, 2800 m, 14 Mar 1954, L. Valcarcel 3, 11, 12 (FH). BRAZIL. RÍO DE JANEIRO: Parque Nacional do Itatiaia, along entry road near border with Minas Gerais between km 9 and

km 10, 22°22'S, 44°45'W, 2200–2240 m, humid roadsides near upper limit of continuous forest, 06 Jul 1991, D. Vital (SP). ECUADOR. AZUAY: along the road to Limón, 8900 ft. 31 Jan 1974, M. King 6633F (MO); PICHINCHA: along road 71 from Interamerican Highway toward Santo Domingo de los Colorados, 0°20'S, 78°40'W, 6 Jun 1975, M. Crosby 10519, 10500 (MO).

DISTRIBUTION AND HABITAT

Pohlia papillosa is distributed from Mexico to central Argentina and Chile through the Andean corridor and Brazil. *Pohlia elongata* and *P. papillosa* are the most frequent species of *Pohlia* from Neotropical montane forests and páramo. It grows on soil, in exposed places or flanked by rocks, between 1400–3500 m, reaching in Argentina 6030 m (Schiavone & Suárez, 2009). The distinctiveness of this species is the exothelial cells, which are isodiametric to short-rectangular with strongly bulging walls. When plants are sterile, they are easily distinguishable by the abundance of axillary propagula. Propagula are linear or vermicular, hyaline, although there are also oblong or obconic; they are slightly orange and always show poorly-developed leaf primordia.

Pohlia apolensis is another Neotropical species with bulging exothelial cells, which is easily identifiable by its reddish color and foliar primordia with incurved apices. It is a very variable species regarding both the arrangement of its leaves and the density of its propagula. When grown in protected sites with greater availability of water, the plants have leaves loosely arranged, abundant vermicular and hyaline propagula and are always sterile. Within the species, it also presents a marked variability in the length of setae, i.e., from 14 to 40 mm in length, in the same population.

NOMENCLATURE

Pohlia papillosa was originally described as *Bryum papillosum* by Müller (1848) on the basis of a single specimen collected by Funck and Schilm in Colombia. However, this name is illegitimate as a posterior hom-

onym of *B. papillosum* Dicks. of 1801, and Jaeger (1875) legitimized the epithet *papillosum* when transferring *Bryum papillosum* to the genus *Brachymenium*. Apart from the type specimen of *Bryum papillosum* Müll. Hal., he added to the protologue four specimens collected by Spruce (373, 374, 375, 376) in the Andean area of Ecuador in 1862 and one specimen of Lindberg from Colombia in Bogota. It was Brotherus (1903) who transferred it into *Pohlia*. The syntypes collected by Spruce are preserved in BM. Numbers 373 and 376 are complete plants with typical characters of the species, number 375 contains only a few plants of *P. papillosa* mixed with another moss, number 374 are clearly identifiable plants, though incomplete. The lectotype selected by Shaw (1982) is deposited in NY.

As a result of these studies, two new synonyms: *P. longipedicellata* (Müll. Hal.) Broth from Venezuela and *P. verrucosa* (Müll. Hal.) Broth from Bolivia have proposed. *Pohlia longipedicellata* is known only from the original collection and has the typical characteristics of *P. papillosa*. The type specimens have long setae like those plants growing in sheltered and wetter places, with oblong propagula with well-developed leaf primordia. Isotypes of this species are in BM, H, NY and PC, and we designated here the lectotype at BM. Ochi (1981) synonymized this name under *P. flexuosa*, a species previously restricted to Europe (Shaw, 1982) and recently recorded in the U.S.A. (Shaw & Toren, 2009), which in turn is characterized by free sharp peristome teeth, different from the blunt teeth fused at the base of *P. longipedicellata*.

The type specimen of *P. verrucosa* has propagula of both types (oblong and elongate), as some specimens from Brazil. While *P. verrucosa* does not present the typical form of *P. papillosa*, the species maintains the specific character. Isotypes of the species are found in H and NY, designating here the specimen at H as the lectotype.

Bryum anisodontacum is recorded in Chile, South America. The plants deposited in BM are mostly sterile with abundant

propagula, identical to the plants from the páramo in Ecuador and Colombia. Examination of material of Dusén shows that the specimen belongs to *P. papillosa*, recorded for the first time as a species from Chile.

Pohlia pseudobarbula (Thér.) H. A. Crum ex A. J. Shaw, Contr. Univ. Michigan Herb. 15: 254. 1982. ≡ *Webera pseudobarbula* Thér., Smithsonian Misc. Collect. 85(4): 28 f. 17. 1931. Type: MEXICO, Desierto, Bro. Amable 1630 (FH!). (Figures 6(C), 15(A-I), 16).

Plants small, green to yellow-green, opaque. Stems 5–15 mm long, reddish, simple or branched by 1–4 innovations, in cross section rounded to elliptical, with central strand well developed. Axillary hairs 75–185 μm long, with 2 brown basal cells and 1–3 distal hyaline cells. Leaves equally distributed along stem, flexuose when dry, erect to erect-spreading when wet, 1.0–1.2 \times 0.2–0.3 mm, lanceolate; apex acute; margins revolute, serrulate towards apex; costa robust, ending before the apex, red only at the base; laminal cells thin-walled, the apical ones long-rhomboidal, 27–80 \times 6–12 μm , median cells long-rhomboidal to fusiform, 50–105 \times 5–12 μm , basal cells short-rectangular, 20–65 \times 7–13 μm . Propagula scarce, 150–250 μm long, ovoid-spherical obconical, red or orange, with 2–5 apical or subapical leaf primordia. Dioicous. Perichaetial leaves, ovate-lanceolate to lanceolate, 1.1–3.0 \times 0.3–0.4 mm. Setae one per perichaetium, 20–25 mm long, reddish brown; capsule inclined, long-pyriform, 2.8–3.1 \times 1.0 mm, with neck poorly differentiated; exothecial cells short- to long-rectangular, walls flexuose, 40–93 \times 15–40 μm ; stomata phaneroporous; annulus of 1–2 rows of rounded vesicular cells; exostome teeth whitish to hyaline, 230–260 μm long, entire to sparsely bordered, slightly trabeculate papillose; endostome papillose hyaline, 220–250 μm long, basal membrane low, 1/3 the length of the endostome, segments weakly perforate, cilia absent. Operculum conical. Spores 13–20 μm in diameter, smooth.

SPECIMENS STUDIED

MEXICO. PUEBLA: Chignahuapán, along route 119, 18°50'N, 98°00'W, 10100 ft., vertical bank, 11 Feb 1975, F. Hermann 26450 (MO); MICHOACÁN: vicinity of Morelia, Campanario, 2200 m, 09 Dec 1911, G. Ar-sène 7553 (B).

DISTRIBUTION AND HABITAT

Pohlia pseudobarbula is an endemic species from Mexico, with few records in this country. It grows mixed with *Anomobryum filiforme*. The narrow cylindrical capsule with smooth rectangular exothecial cells is a distinctive trait of *P. pseudobarbula*; it differs from *P. apolensis* and *P. papillosa*, other two Neotropical propaguliferous species, in that the capsules are pyriform with mammillose exothecial cells. However, these set of species share one trait: rounded exostome teeth, trabeculate, not bordered.

NOMENCLATURE

This species was described by Thériot (1931) as *W. pseudobarbula*, based on four specimens collected by Brother Amable in different locations in Mexico (Bro. Amable 1630, 1643, 1658 and 1684). In his thesis, Crum (1951) proposes transferring it to the genus *Pohlia*, but it is Shaw (1982) who made the combination.

Pohlia wilsonii (Mitt.) Ochyra, Ill. Moss Fl. Antarctica. p. 433. 2008.

≡ *Bryum wilsonii* Mitt., Hooker's J. Bot. Kew Gard. Misc. 3: 55, 1851. ≡ *Brachymenium wilsonii* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 112. 1875. ≡ *Webera wilsonii* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 112. 1875. ≡ *Leptobryum wilsonii* (Mitt.) Broth. Nat. Pflanzenfam. I(3): 546. 1903. ≡ *Wollnya wilsonii* (Mitt.) Herzog, Beih. Bot. Centralbl., Abt. 2, Systematik 28 ((2)): 271. 1911. Type: ECUADOR. Quito, Jameson s/n (Isotype: BM!, S!). (Figures 1(A,B) 2(B), 17(A-J), 18)

Leptobryum pottiaeum Dusén, Rep. Princeton Univ. Exp. Patagonia, Botany 8: 87. f. 15; 9 f. 10–12. 1903. Lectotype: Patagonia

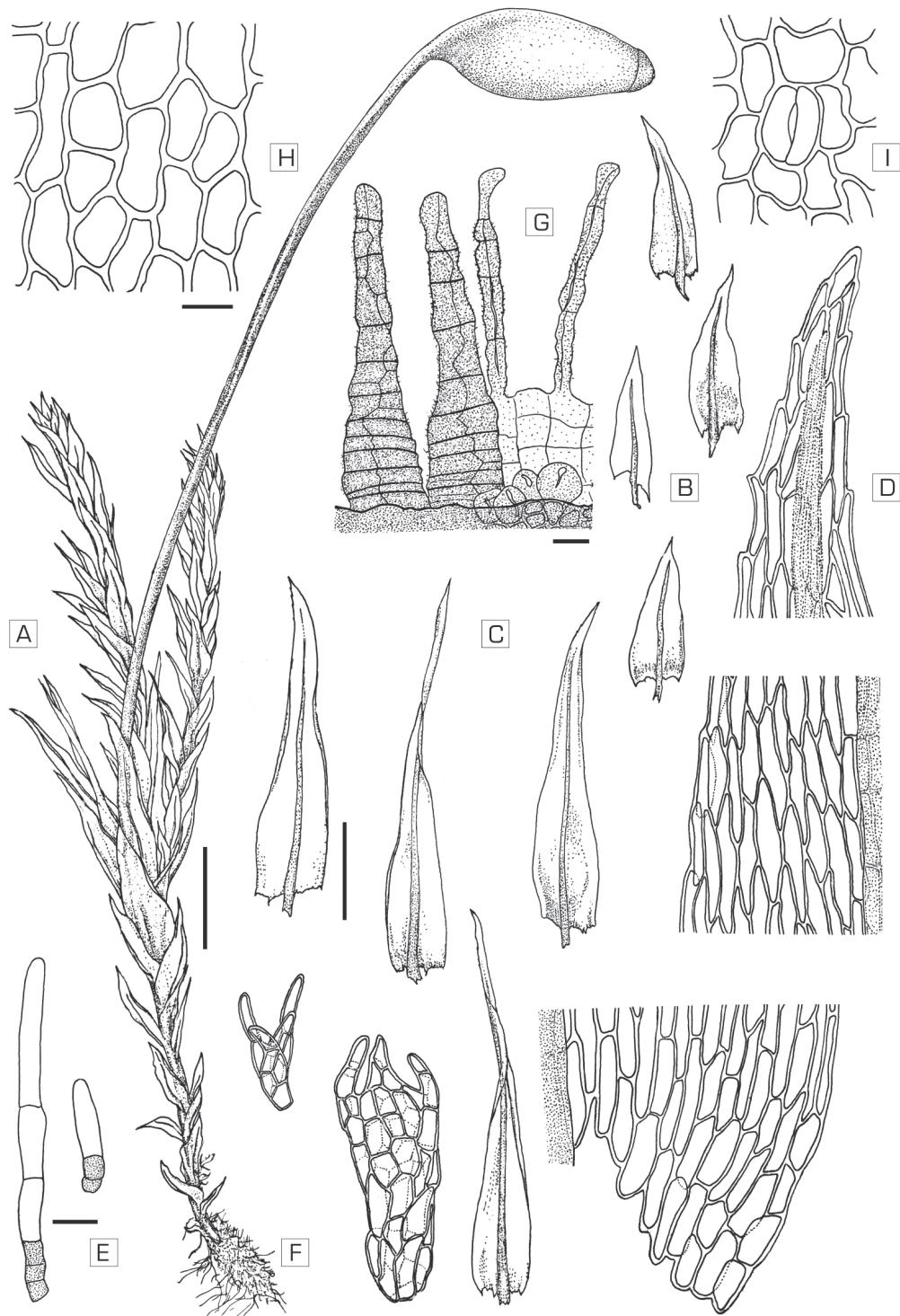


Figure 15. *Pohlia pseudobarbula*. A – Habit in wet, B – Leaves, C – Perichaetial leaves, D – Apical, median and basal cells, E – Axillary hairs, F – Propagula, G – Peristome, H – Exothecial cells, I – Stoma. Scale bars: A = 1 mm; B, C = 0.5 mm; D-I= 25 μ m.

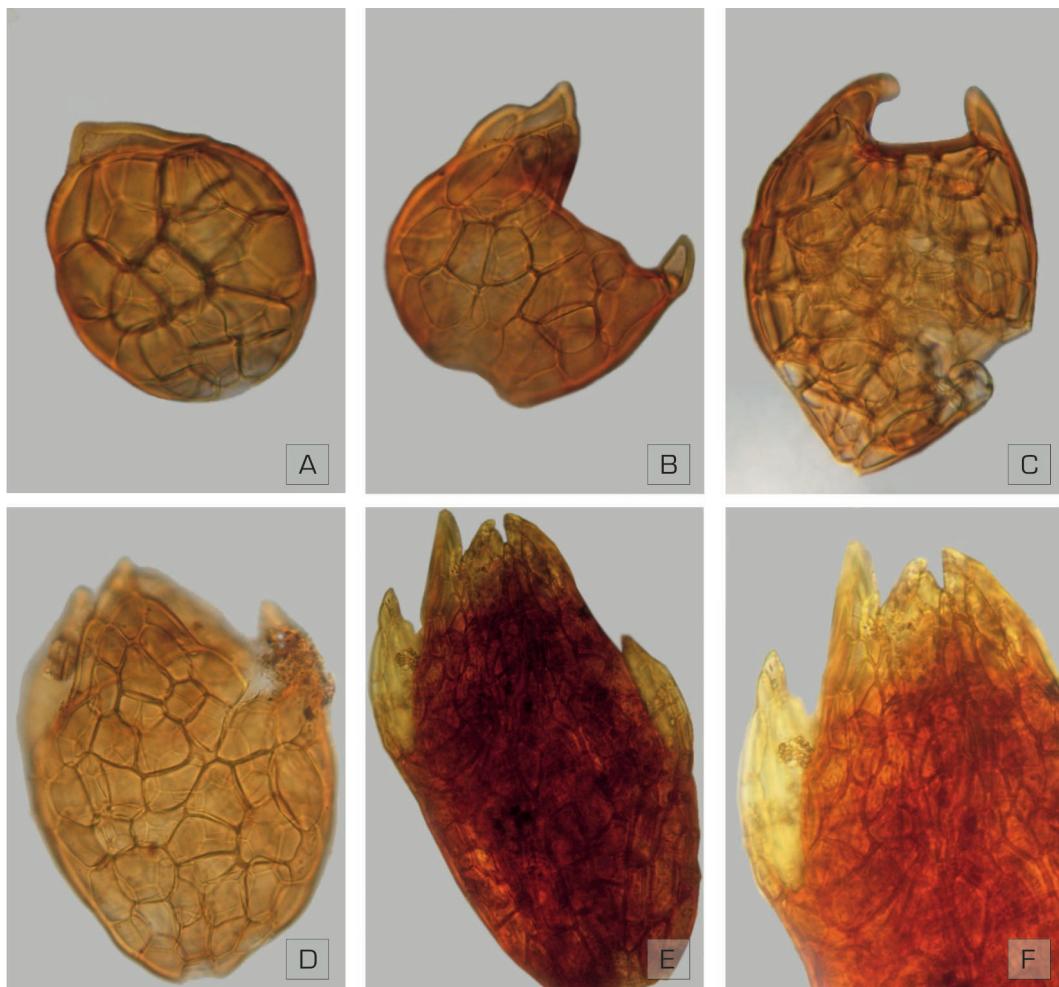


Figure 16. *Pohlia pseudobarbula*. Propagula. Scale bars = 40 μm .

australis in territorio Fontanali fluminis Río Chico in truncis putridis et in terra (no seen). Sintype: Fuegia australis ad Lapataia in terra (NY, no seen)

Wollnya stellata Herzog, Beih. Bot. Centralbl., Abt. 2, Systematik 26 (2): 69. 3. 1910. \equiv *Leptobryum stellatum* (Herzog) Broth., Nat. Pflanzenfam. ed. 2, 10: 374. 1924. Type: Bolivia. An feuchten Felsen im Llavatal bei Cochabamba ca. 3800 m; Januar, 08., Th. Herzog (JE-Herzog, no seen)

Webera integra Cardot, Rev. Bryol. 38: 4. 1911. \equiv *Pohlia integra* (Cardot) A. J. Shaw, Contr. Univ. Michigan Herb. 15: 285. 1982. \equiv *Mniobryum integrum* (Cardot) Broth. Nat. Pflanzenfam. (ed. 2), 10: 362. 1924. Type:

MEXICO. wet rocks, 8000 ft., Jan 1909, C. Purpus 3715 (FH!, BM!).

Leptobryum escomelli Thér., Bryologist 25: 30. 1922. Lectotype: Peru, Jura près d’Arequipa, Edm. Escomel, 1921 (isotype in S, no seen)

Mniobryum bracteatum E.B. Bartram, Rev. Bryol. Lichénol. 6: 9–18. 1934. Type: ECUADOR. Napo province, banks of river Napo, M. Villavicentia s.n. (FH!).

Mniobryum aspillaiae Thér., Revista Chilena de Hist. Nat. 28: 132. 1924. Type: CHILE. Grotte de Tanumé, 20 Jan 1917, C. Aspilla (H!).

Plants small to medium-sized, pale green to yellowish green, glossy. Stems 8–12 mm long, light green, simple, in cross section rounded, with central strand. Axillary hairs 95–125 µm long, with 2–4 basal brown cells and 1 distal hyaline cell. Leaves equally distributed along stem, flexuose when dry, spreading when wet, 1.0–1.8 mm, ovate to ovate-lanceolate; apex acute; margins flat to weakly reflexed, entire to serrate near the apex; costa robust, subpercurrent, green, divided in the apex; laminal cells thin-walled, lax, apical cells long-hexagonal to long-rhomboidal, 27–93 × 10–20 µm, median cells rectangular to long-hexagonal, 57–137 × 16–25 µm, basal cells small, wide-rectangular, 46–137 × 11–26 µm. Rhizoidal propagula abundant, reddish brown, ellipsoidal to rounded, 60–330 µm long. Dioicous. Perichaetial leaves longer than vegetative ones. Setae 1 per perichaetium, 10–33 mm long, reddish-brown; capsule erect to inclined, short-pyriform, 1.4–2.0 mm long, with neck as long as the urn; exothelial cells small, thin-walled, irregularly short-rectangular isodiametrical, 17–57 × 15–32 µm; stomata scarce, cryptoporous; annulus 1 row of rectangular vesiculose cells, partially deciduous; exostome teeth yellowish-brown above, 370–400 µm long, lanceolate, trabeculate, entire to sparsely perforate, strongly papillose; endostome yellow, 350–390 µm long, finely papillose, basal membrane low, segments narrowly perforate, cilia absent. Operculum conical. Spores 12 µm in diameter, papillose.

SPECIMENS STUDIED

SOUTH AMERICA. ECUADOR. QUITO: Near Quito; Valley of Machachto, 3000 m, 25/12/1971, P. C. Koopman (0411137 L); 25/12/1971, P. C. Koopman (0411134 L). PERU. CUZCO: Pcia. Quispicanchis, Loc. exacta Ceateca, 3700 m, C. Vargas 2201 (FH) as *Pohlia vargasii* sp. nov. CHILE. CHILOE: J Hamilton in Herb. H. N. Dixon 418 (L) as *Pohlia hamiltonii* sp. nov. ARGENTINA. SALTA: San Antonio de Los Cobres, alrededores del Volcán Socoma, 3576 m, 24°32'S, 68°12'W, 03 Apr 2005, G. Suárez

454, 455, 456 (LIL); TUCUMÁN: Tafí del Valle, arroyo afluente río «Los Zarzos», El Pichao, 26°21'11"S, 66°02'45"W, 2345 m, 20 May 2005, G. Suárez 474 (LIL), Ruta Provincial 307, km 87, 26°43'S, 65°47'W, 2982 m, 18 May 2005, G. Suárez 457, 458, 460, 462, 464 (LIL).

DISTRIBUTION AND HABITAT

Pohlia wilsonii is distributed from Mexico, Ecuador through the Andean corridor to the southern extreme of Chile and Argentina and Africa. It grows in exposed places close to watercourses or the sheltered by rock. In Argentina, it has been collected in high Andean environments from the province of Salta to the province of Mendoza.

Plants growing in sunny sites constitute much more dense populations and their leaves are densely imbricate. However, when the populations grow near melting ice or water courses, the communities are more lax and the leaves are arranged loosely. The traits that characterize *P. wilsonii* are the yellowish-green color of the plants, lax laminal cells and, mainly, the presence of rhizoidal tubers.

NOMENCLATURE

Bryum wilsonii was described by Mitten in 1851 on the basis of materials collected in Quito, Ecuador. Subsequently, Jaeger (1875) transferred it to the genus *Brachymenium*, Webera, and finally Brotherus (1903) included it in the genus *Leptobryum*, its main trait being the long and well-developed endostomial cilia. The current combination was fully justified by morphological and cytological evidence by Ochyra *et. al.* (2008) and its phylogenetic position within *Pohlia* was confirmed by parsimony analyses (Suárez, 2008). On the other hand, *Mniobryum aspillagae* was described by Thériot (1924) from Chile and recently synonymized with *P. wilsonii* (Suárez & Schiavone, 2008b). The type specimen of this species, which consists of plants with sporophytes, is deposited in H. In FH, the herbarium name *Pohlia vargasii* was found in FH. This material, collected by C. Vargas 2201 in Peru in the town of

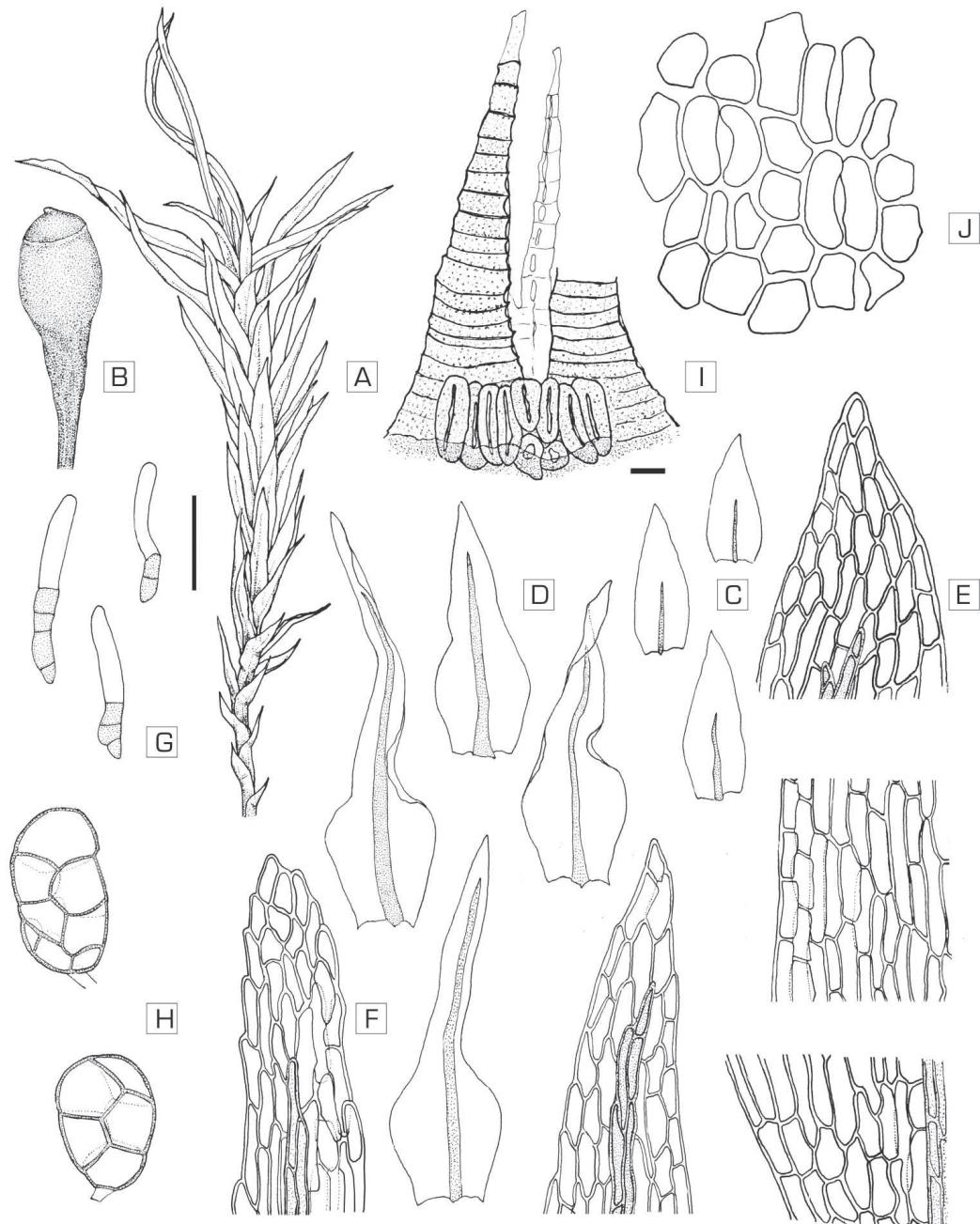


Figure 17. *Pohlia wilsonii*. A – Habit in wet, B – Sporophyte, C – Leaves, D – Perichaetial leaves, E – Apical, median and basal cells (leaves), F – Apical cells (perichaetial leaves), G – Axillary hairs, H –Propagula, I – Peristome, J – Stoma. Scale bars: A, B = 1 mm; C-I = 25 μ m.

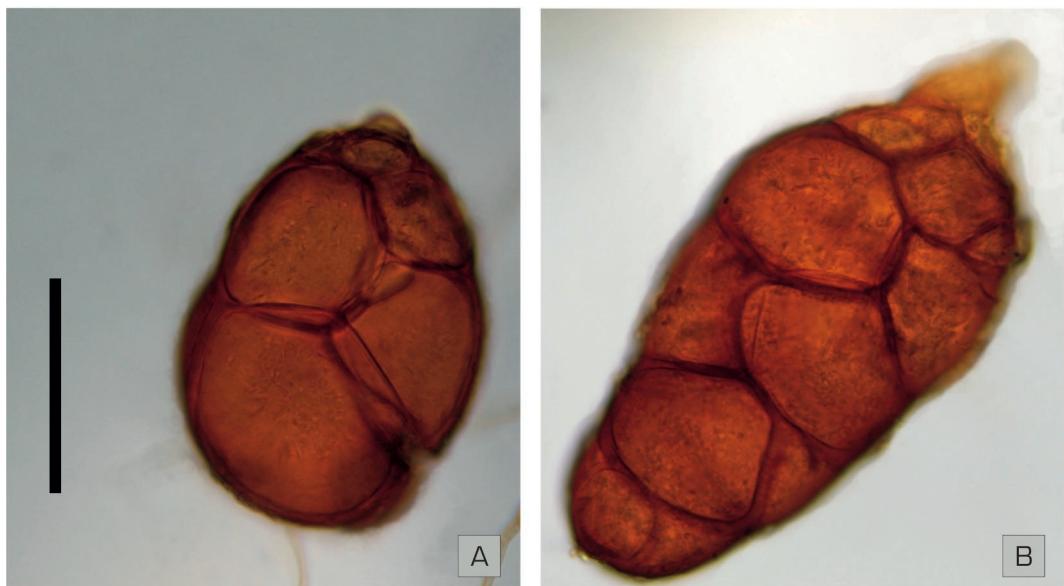


Figure 18. *Pohlia wilsonii*. Propagula. Scale bars = 50 µm.

Ceatec, corresponds to *P. wilsonii*. A similar situation occurs with a specimen collected for J. Hamilton 418 in Chiloé and deposited in L. This plant was nominated by Dixon as «*P. hamiltonii*», but it was never published. This herbarium name also corresponds to *P. wilsonii*.

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