

A preliminary treatment of the *Holomitrium* complex (Musci: Dicranaceae) in Central America

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Abstract. The *Holomitrium*-complex (consisting of *Holomitrium*, *Eucamptodontopsis*, and *Schliephackea*) is a group of closely related genera in the Dicranaceae characterized by five features: 1. a strong single costa, 2. well developed alar cells, 3. long, sheathing perichaetial leaves, 4. erect capsules, and 5. undivided peristome teeth. *Holomitrium sinuosum* is newly described. *Dicranoloma brittonae* is transferred to *Eucamptodontopsis*. *Holomitrium standleyi* is a synonym of *H. arboreum*. *Breedlovea chiapensis* is a synonym of *Holomitrium pulchellum* and the genus *Breedlovea* is placed into the synonymy of *Holomitrium*.

In terms of species numbers the Dicranaceae represents the largest family of Central American mosses. The family exhibits a considerable amount of generic variation, consequently most of its genera are not difficult to recognize. But, there are also groups of genera within the family that are not easy to distinguish. One such group consists of the genera *Holomitrium*, *Eucamptodontopsis* and *Schliephackea*; a group nomenclaturally centered on *Holomitrium*.

The members of this complex are medium to large sized, acrocarpous mosses. They are commonly corticolous, growing on tree trunks, upper branches and the on the roots of epiphytic plants. Occasionally they are found growing terrestrially or on rocks, but these types of habitats seem to be secondary, i.e. they appear to represent an originally corticolous population that has become established on the ground as result of a tree or branch fall. This generic complex is marked by five morphologically features: 1. a strong single costa, 2. well developed

alar cells, 3. long, sheathing perichaetial leaves, 4. erect capsules, and 5. undivided peristome teeth.

There are few unique characters separating the genera of this complex. Furthermore, some of the features that appear to be characteristic of one member of the group commonly can be found sporadically throughout the complex, thus weakening the internal generic boundaries of the complex. The following two examples illustrate this problem. Within *Eucamptodontopsis* the leaves are tightly, spirally contorted when dry, while in *Holomitrium* the leaves are characteristically crispate when dry. However, in two species of *Holomitrium* as well as in *Schliephackea* the leaves are variably spirally contorted when dry. *Holomitrium* is best recognized by the sharp contrast in size and shape between its upper and lower leaf cells. The upper cells are generally short and straight-walled while the lower leaf cells are elongate and porose. Species of *Eucamptodontopsis* and *Schliephackea* have elongate, porose

cells throughout the leaf. However, *H. terebellatum* and *H. flexuosum* have weakly differentiated upper and basal leaf cells and in *H. sinuosum* leaf cell differentiation is essentially absent.

Key to the Holomitrium-complex in Central America.

1. Plants pendant; leaves widely spaced, spreading-recurved from base, margins serrate 3. *Schliephackea*
1. Plants erect; leaves crowded, erect at base, margins serrate or crenulate 2.
2. Leaves crispate when dry with serrate or crenulate margins OR leaves spirally-crispate when dry with serrate margins; upper and lower leaf cells sharply differentiated (except in *H. sinuosum*) 2. *Holomitrium*
2. Leaves spirally contorted when dry with crenulate margins; lower leaf cells grading uniformly into the upper leaf cells 1. *Eucamptodontopsis*

1. *Eucamptodontopsis* Broth., Nat. Pflanzenfam. 10: 202. 1924.

Type species: *E. pilifera* (Mitt.) Broth.

Plants medium to large, stems erect, branches few, irregularly spaced, in cross-section with a small central strand; stem moderately to sparsely tomentose. Leaves spirally contorted above. Leaf cells elongate and porose throughout. Alar cells well-developed. Perichaetial leaves long-sheathing. Setae long. Capsules erect, cylindrical, Peristome teeth undivided.

Eucamptodontopsis is a neotropical genus of three species. In Central America the genus is distinguished from *Holomitrium* by the combination of its spirally contorted leaves and crenulate leaf margins. Most *Holomitrium* species have leaves that are crispate when dry, while those species with weakly spirally contorted leaves have serrate leaf margins. *Schliephackea* also can have spirally contorted leaves but the leaf margins are serrate, it also differs from *Eucamptodontopsis* in its pendant habit and its widely spaced leaves that are strongly spreading from the base. In *Eucamptodontopsis* the leaves moderately spaced, and the plants as well as the leaf bases are erect.

The three species of *Eucamptodontopsis* are distinguished in the following key.

Key to the species of *Eucamptodontopsis*

1. Leaf apices hyaline; leaves broadly ovate-acuminate, up to 5 mm long *E. pilifera* (Caribbean, Surinam, Venezuela)
1. Leaf apices concolorous, leaves linear-lanceolate from a short ovate base, leaves 7-15 mm long 2.
2. Plants to 12 cm high; leaves >1 mm wide at base, spirally contorted only in the upper half; leaf margins remotely denticulate above; leaves 10-15 mm long *E. brittonae* (Costa Rica, Panama)
2. Plants to 4 cm high; leaves <1 mm wide at base, spirally contorted from just above the leaf base; leaf margins entire; leaves 7-10 mm long *E. tortuosa* (Venezuela)

1. *Eucamptodontopsis brittonae* (Bartr.) Allen, comb. nov. *Dicranoloma brittonae* Bartr., Contr. U.S. Natl. Herb. 26: 69. 1928. Type. Costa Rica, Heredia: Cerros de Zurquí, northeast of San Isidro, Standley & Valerio 50505 (isotypes F, NY, US).

Plants medium to large, in loose, yellowish-green tufts, corticolous, occasionally humicolous. Stems erect, 10-12 cm long. Leaves evenly spaced, moderately crowded, erect-spreading below, spirally contorted above when dry, concave to tubulose, linear-lanceolate, 10-15 mm long, apex tubulose-setaceous, base shortly clasping, margins broadly incurved, remotely crenulate above, entire below. Costa single, smooth to slightly roughened at back above, percurrent. Upper laminal cells linear-rectangular; those at the margins distinctly shorter, more or less rhomboidal, walls incrassate and pitted, smooth; basal cells linear-rectangular, not sharply differentiated from the upper leaf cells, walls incrassate and pitted, smooth; alar cells strongly differentiated, incrassate, short-rectangular, reddish-brown, walls incrassate, weakly pitted. Sporophytes unknown.

Illustrations. Bartram (1928, Fig. 11, A-I).

Distribution in Central America. Costa Rica (Alajuela, Heredia, Puntarenas, San José); Panama (Bocas del Toro, Chiriquí, Coclé, Panama, Veraguas).

Habitat. On trunks and upper tree branches, occasionally on humus; 550-2400 m.

Specimens examined. COSTA RICA. Alajuela: La Palma de San Ramón, Brenes 16206.1 (NY); Heredia: Cerros de Zurquí, Standley & Valerio 50505 (F, NY, US); Puntarenas: Monteverde, Herrera 1106 (NY), James 1969-11 (US), Gentry & Burger 2749D (MO); San José: La Palma, Valerio 141 (US), La Hondura, s. coll. 24 (F). PANAMA. Bocas del Toro: Cerro Colorado, Allen 5044, 5062, 5070, 5101, 5147, 5298, 5230, 5233, 5302 (all MO),

continental divide at Fortuna, Allen 5624 (MO); Chiriquí: N of Cerro Pate Macho, 8°48'N, 82°24'W, Hammel et al. 14407 (MO); Cerro Colorado, ca 4.3 above Camp Chami, Allen 5381 (MO); Coclé: La Mesa, 8°37'N, 80°07'W, McPherson 11245G (MO), El Valle de Anton, Brako 8398a, 8413 (NY); Panama: Cerro Jefe, Allen 4909, 4911, 4930, 4935, Crosby 10903, McPherson 6855A, Stimson 5413 (all MO); Veraguas: Cerro Arizona above Santa Fe, Hammel & Kress 8578 (MO, NY).

Bartram (1928) was unsure of the generic placement of this species which he described as a *Dicranoloma* on the basis of its elongate, pitted, upper leaf cells and narrow marginal cells. Although the marginal cells are narrow in *E. brittonae*, they are not hyaline or sharply differentiated from the inner cells as is typical for species of *Dicranoloma*. In fact, the marginal cells in this species are less differentiated than can be seen, for example, in the marginal cells of *Dicranum majus*. Spirally contorted leaves, leaf cells that are elongated and pitted throughout and smooth to irregularly crenulate leaf margins are indicative of the genus *Eucamptodontopsis*.

Eucamptodontopsis brittonae can be difficult to distinguish from *Holomitrium sinuosum* since the latter species has irregularly crenulate lower leaf margins and leaf cells that are porose to sinuose throughout. In *H. sinuosum*, however, the upper most leaf margins are serrate, the leaves are crispate when dry and broadly ovate at base, the upper leaf cells are rectangular, and the alar cells, at times, are fugacious. While the spirally contorted leaves in *E. brittonae* are narrower at base, the leaf cells are more elongate, the leaf margins crenulate throughout and the alar cells are persistent. As noted above, *E. brittonae* is separated from *Schliephackea meteoroides* by its erect habit and irregularly crenulate leaf margins.

2. *Holomitrium* Brid., Bryol. Univ. 1: 226. 1826.

Type species: *H. vaginatum*, *H. peri-*

chaetiale.

Breedlovea Crum, Bryologist 89: 23. 1986. *syn. nov.*

Type species: *B. chiapensis*.

Plants small to robust, stems erect, branches few, irregularly spaced, in cross-section with a small central strand, enlarged, thick-walled cortical cells, and a smaller, thick-walled epidermis, moderately to densely tomentose. Leaves usually erect at base and more or less clasping, keel or concave above, margins serrate to crenulate, occasionally nearly smooth, erect spreading when wet, crispate (rarely somewhat spirally contorted) when dry. Leaf cells smooth, basal cells elongate and porose, generally sharply differentiated from the shorter, firm-walled upper leaf cells; alar cells differentiated, persistent or fugacious. Costae single, strong, percurrent or excurrent, smooth at back or with a few teeth at back near the apex. Pseudautoicous. Perigonia on dwarf males borne on the female plants. Perichaetial terminal. Perichaetial leaves sheathing to convolute at base, long setaceous above, reaching from 1/2 to the entire length of the setae and at times overtopping the capsules. Capsules exerted, erect, cylindrical to oblong. Opercula subulate-rostrate. Peristome single, the teeth undivided to more or less fenestrate, densely papillose on the outer surface. Annulus absent. Calyptrae long, cucullate, smooth. Spores spherical, weakly papillose.

Key to *Holomitrium* in Central America

1. Leaf margins subentire throughout or crenulate below, serrate at extreme apex 2.
 1. Leaf margins sharply serrate from below midleaf to the apex 3.
 2. Upper leaf cells quadrate with straight walls; alar cells fugacious; leaf margins

subentire; setae 5-10 mm long 3. *H. pulchellum*

2. Upper leaf cells elongate with sinuose walls; alar cells persistent; leaf margins crenulate; setae 10-15 mm long..... 4. *H. sinuosum*

4. *H. sinuosum*

3. Quadrate upper leaf cells extending downward along the margins into the basal region; leaf cells at basal margins quadrate to rectangular, wider than the inner basal cells, and smooth to weakly porose 1. *H. arboreum*

3. All quadrate upper leaf cells ending at same level in the lower leaf; leaf cells at basal margins elongate to linear, narrower than the inner basal cells and porose 4.

4. Alar cells fugacious; upper leaf cells elongate, the outer cells walls sinuose 5. *H. rebellatum*

4. Alar cells persistent; upper leaf cells quadrate with straight cell walls 5.

5. Upper leaves over 10 mm long; leaves gradually narrowed from an oblong base, unistratose throughout; costae shortly excurrent 2. *H. longifolium*

2. *H. longifolium*

5. Upper leaves less than 7 mm long; leaves abruptly narrowed from an ovate base, bistratose at margins and medially in rows; costae percurrent 6. *H. williamsii*

1. *Holomitrium arboreum* Mitt., J. Linn. Soc., Bot. 12: 58. 1869. Types. Peru, Andes Peruvianae, in monte Campana, *Spruce* 22 (F, NY); Ecuador, Andes Quitenses ad fl. Bombonsasa et in sylva Canelos, *Spruce* 22b (NY).
Holomitrium standleyi Bartr., Contr. U.S.

Natl. Herb., 26: 66. 1928. Type. Costa Rica, Guanacaste Prov., Quebrada Serena, SE of Tilarán, *Standley & Valerio 46271* (holotype FH, isotypes NY, US). Paratypes: *Standley & Valerio 45933* (NY, US), *Standley & Valerio 46260* (NY, US). *syn. nov.*

Plants medium, tufted, yellow-green to brownish, corticolous or humicolous. Stems erect, 2-4 cm long, branches irregular. Leaves crowded, spreading when wet, strongly crisped when dry, keeled above more or less clasping at base, leaves long linear-lanceolate from an erect, ovate clasping base, 2-6 mm long, apex acuminate, base clasping, margins plane, strongly dentate in the upper 2/3. Costa percurrent to shortly excurrent, frequently toothed above on dorsal surface. Upper laminal cells subquadrate, walls thickened and straight, smooth, extending downward along the margins into the basal region, basal cells linear, strongly differentiated, walls incrassate, pitted, basal marginal cells short rectangular not or weakly porose, wider than the inner basal cells, alar cells differentiated, forming distinct groups of enlarged, red-brown thin-walled cells. Perichaetial leaves frequently reaching the base of the capsules. Setae 1-2 cm long. Capsules cylindrical, 4-5 mm long. Stomata phaneropore. Peristome teeth linear-lanceolate, papillose undivided to irregularly fenestrate, 0.4-0.5 μm high.

Illustrations. Bartram (1928, Fig. 9, as *H. standleyi*); Bartram (1949, Fig. 28, a-f).

Distribution in Central America. Belize (El Cayo, Toledo); Guatemala (Alta Verapaz, Baja Verapaz, Huehuetenango, Jalapa); Honduras (Atlántida, Comayagua, Morazán); Costa Rica (Alajuela, Cartago, Guanacaste, Heredia, Limón, Puntarenas, San José); Panama (Bocas del Toro, Chiriquí, Cocle, Colón, Darien, Panama, Veraguas).

Habitat. Corticolous on branches, trunks and stumps, occasionally on granitic or limestone rocks, rarely terrestrial; sea level-1750 m.

Selected specimens examined. BELIZE. El Cayo: Pine Ridge Bartlett 11691 (MO, US), San Agustín, Mains 3876 (F, US); Toledo: beyond Union Camp, Edwards Road beyond Columbia, Gentle 6499 (MO). GUATEMALA. Alta Verapaz: north of Coban, Sharp 2956 (MO, NY, US); Baja Verapaz: Santa Rosa, Türckheim 6909 (NY); Huehuetenango: above Puente Alto, Sharp 4905 (F); Jalapa: Cerro Alcoba, Steyermark 32552 (F). HONDURAS. Atlántida: Lancetilla Valley, near Tela, Standley 54188 (F, US); Comayagua: Siguatepeque, Olsen 84-12 (MO); Morazán: La Montanita, Standley 12364 (F). COSTA RICA. Alajuela: La Palma de San Ramon, Brenes 16219a (NY); Cartago: El Muneco, Standley & Torres 50893 (US, NY); Guanacaste: Tilarán, Alfaro 120 (US); Heredia: north of Varablanca, Crosby 3884 (MO); Limón: 2 km SSE of Islas Buena Vista, 83°40'W, 10°40'N, Davids & Herrera 31048 (MO); Puntarenas: Cordillera de Talamanca, road to Sitio Coto Brus, 8°57'N, 82°46'W, Davids 24574 (MO); San José: La Palma area, 10°03'N, 83°59'W, Crosby & Crosby 6254 (MO). PANAMA. Bocas del Toro: Continental Divide, vicinity of Fortuna, 8°55'N, 82°08'W, Allen 5718 (MO); Chiriquí: Cerro Colorado, 8°35'N, 81°45'W, Allen 5211B (MO); Cocle: near El Valle de Antón, 8°37'N, 80°07'W, McPherson 7658B-2 (MO), Atlantic slope of Continental Divide above El Copá, 8°40'N, 80°36'W, Knapp & Dressler 3484 (MO); Colón: Santa Rita ridge, 9°15'N, 79°40'W, Crosby 10374 (MO); Darien: along Rio Pucuro, 18 km E of Pucuro, 8°05'N, 77°16'W, Hammel et al. 16522 (MO); Panama: Cerro Campana, Stimson 5392A (MO); Veraguas: Escuela Agrícola Alto Piedra, Croat & Folsom 33934 (MO).

Holomitrium arboreum, the most common species of the genus in Central America, exhibits considerable variability in most of its features. But, it can be recognized by the presence of several rows of subquadrate leaf cells that extend downward along the margins from the median region to the basal region of the leaves. This group of subquadrate cells ends in a single row of short, broadly rectangular cells that are smooth or weakly porose and wider than the interior basal cells. In all other Central American species of *Holomitrium* the median and basal cells are either sharply distinguished or the basal cells grade imperceptibly into the median

cells and the basal marginal cells are both narrower and more porose than those of the interior.

In its typical form, the leaves of *H. arboreum* are strongly clasping at base and tightly crispate-curved when dry, the costa is percurrent, the basal marginal cells have straight walls and the upper leaf cells are quadrate. Plants from Costa Rica and Panama commonly have long, crispate leaves that are loosely erect at base, a shortly excurrent costa, weakly porose basal marginal cells and elongate upper leaf cells. This latter expression, described by Bartram (1928) as *H. standleyi*, is striking in its best expression, but there are many collections of intermediate form that link the two expressions.

Collections of *H. arboreum* from Belize and Guatemala commonly have leaves with rows of bistratose cells either medially or on the upper margins. Bistratose leaves of this sort are also found in *H. williamsii* and *H. calycinum*. In both *H. williamsii* and *H. calycinum*, however, the median leaf cells do not run down the basal margins and the basal marginal cells are narrow, elongate and strongly porose.

2. *Holomitrium longifolium* Hampe, Ann. Sci. Nat. Bot. ser. 5, 3:364. 1865. Type. Colombia, Cundinamarca, Alto del Trigo, *Lindig 2116* (not seen).

Plants medium to large, densely tufted, greenish-yellow above, brown below. Stems erect, up to 8 cm long, branches few and irregular, simple. Leaves crowded, erect-spreading when wet, erect at base and crisped above when dry, leaves from an oblong, clasping base gradually narrowed into a long, linear-lanceolate, commonly keeled upper leaf, 10-12 mm long, apex setaceous and fragile, frequently broken, margins plane, sharply serrate to dentate in upper one-half. Costa excurrent, toothed at back above. Upper laminal cells quadrate, homogeneous, walls evenly thickened, the outer walls straight; basal

cells linear, yellow, walls incrassate and pitted, those at the margins narrower than the interior cells, thick-walled and pitted; alar cells persistent, forming distinct groups, rectangular, thin-walled, reddish-yellow. Sporophytes not seen. Illustrations. None.

Distribution in Central America. Costa Rica (Heredia, San José).

Habitat. On trees and open banks; 1750-2000 m.

Specimens examined. COSTARICA. Heredia: Volcán Barba, Valerio C.14 (US), Yerba Buena, northeast of San Isidro, Standley & Valerio 50055 (US), vicinity of Varea Blanca, Croat 35539b, 35554 (MO); San José: Cerros de Zurqui, 10°03'N; 84°01'W, Crosby 9714 (MO).

Holomitrium longifolium is recognized by its long, setaceous leaves. The leaves must be carefully examined however, since they may appear to be much shorter than they actually are due to their frequently broken apices. This species is similar to *H. terebellatum* in leaf shape (weakly clasping and gradually narrowed from an oblong base), plant size and the presence of long, narrow, porose cells along the basal leaf margins. In addition to its larger leaf size, *H. longifolium* differs from *H. terebellatum* in its persistent alar cells and its quadrate upper leaf cells that have firm, evenly thickened walls. In *H. terebellatum* the alar cells are fugacious and the elongate upper leaf cells have sinuose outer walls.

3. *Holomitrium pulchellum* Mitt., J. Linn. Soc., Bot. 12: 60. 1869. Type. Ecuador, Andes Quitenses ad pontem Pastasae dictum Agoyan, *Spruce 26* (NY holotype).

Breedlovea chiapensis Crum, Bryologist 89: 23. 1986. Type. Mexico, Chiapas, SW of Hwy. 190 near Rancho Nuevo, ca 9 mi SE of San Cristóbal las Casas, *Breedlove 15087* (MO isotype). *syn. nov.*

Plants slender, tufted, forming compact cushions, yellowish-green above, yellow-brown below, corticolous. Stems erect, 5-20 mm long, branches irregular, simple. Leaves crowded, erect spreading to flexuous when wet, crisped and contorted, the apices more or less spirally twisted when dry, keeled to canaliculate above, leaves linear-lanceolate, 3-7 mm long, apex acuminate, base weakly clasping, margins erect, entire or weakly crenulate to toothed at the extreme apex, unistratose. Costae smooth at back. Upper laminal cells quadrate to rounded, walls very incrassate but with straight walls, smooth, basal cells linear, strongly differentiated, forming distinct groups, walls incrassate and pitted, smooth, alar cells weakly differentiated fugacious and remaining on stem when leaves are removed, hyaline. Perichaetial leaves reaching half way to the base of the capsule. Setae 5-10 mm long, yellow. Capsules oblong, 1.5 mm long. Stomata phaneropore. Peristome reddish, lanceolate, undivided or irregularly fenestrate, papillose throughout or the papillae arranged in weak vertical rows. Opercula 1 mm long.

Illustrations. Bartram (1949, Fig. 27, D-F); Crum (1986, Figs. 8-11 as *Breedlovea chiapensis*).

Distribution in Central America. Guatemala (Baja Verapaz, Quezaltenango); Costa Rica (San José); Panama (Bocas del Toro, Chiriquí).

Habitat. Corticolous on upper tree trunks and humicolous on the roots of epiphytic canopy plants; 1200-3200 m.

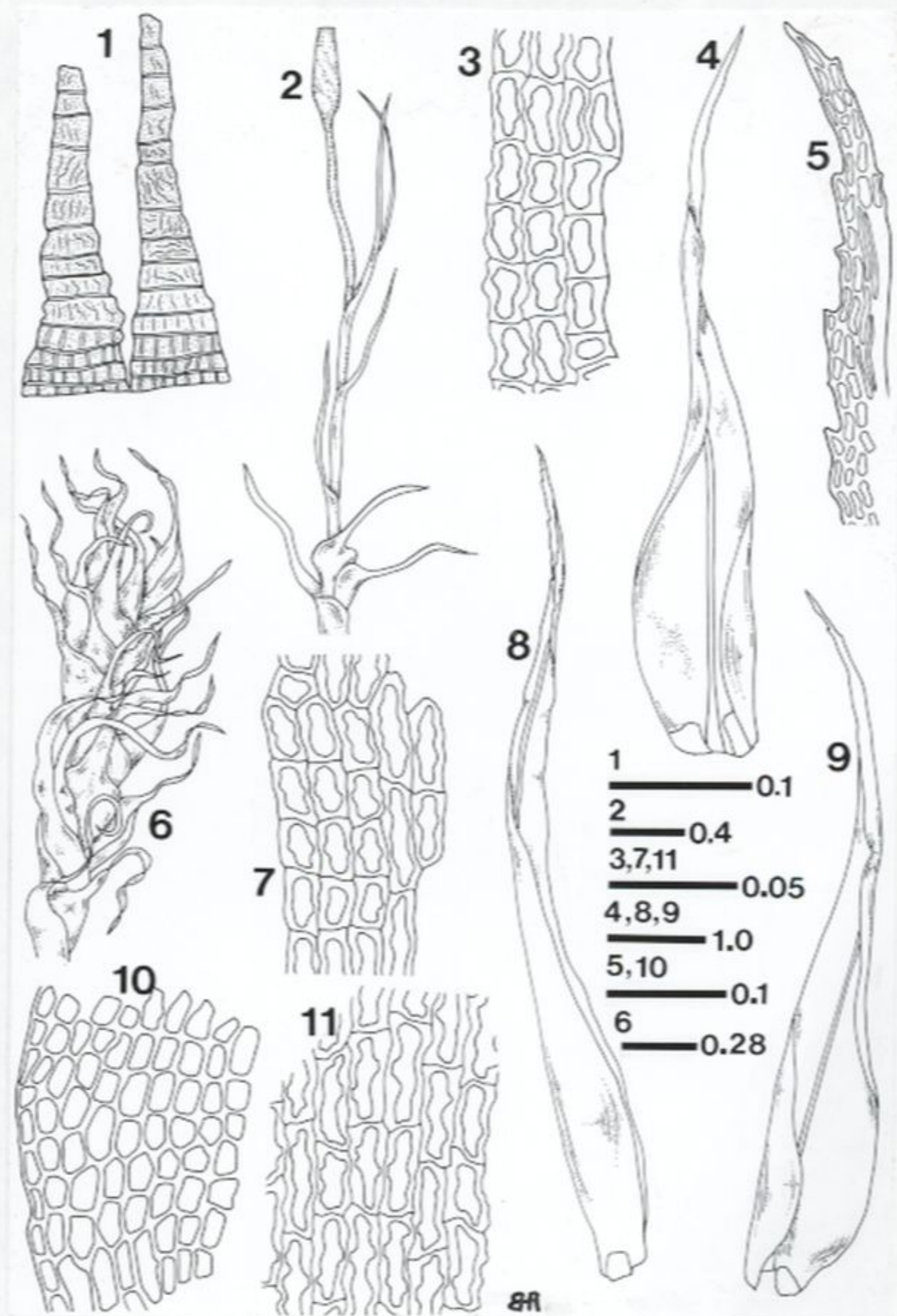
Specimens examined. GUATEMALA. Baja Verapaz: Finca Bucaral, Sharp 2759 (US); Quezaltenango: above Chiquival, Sharp 2199a (US). COSTA RICA. San José: 97 kms S of Cartago along the Panamerican Highway, Griffin et al. 481 (MO, US). PANAMA. Bocas del Toro: between Itamut & Bine peaks, Fabrega massif, Gómez et al. 22492, 22519 (F, FH, MO, NY, US); Chiriquí: vic. of Gualaca, Antonio 5017 (MO), Cerro

Colorado, 8°35'N; 81°45'W, Allen 5418 (MO, NY, US), Allen 5422 (MO, NY).

Holomitrium pulchellum is the smallest member of the genus in Central America, and along with *H. sinuosum* is the only species with entire to irregularly crenulate leaf margins. All other Central American species of *Holomitrium* have serrate to dentate leaves in the upper half of the leaf. The alar cells of *H. pulchellum* are poorly developed and commonly fugacious. They may be absent or present only as a single row of differentiated cells. This character state is also found in *H. terebellatum* and to a lesser degree in *H. sinuosum*. The latter two species, however, are larger plants with generally excurrent costae and leaf cells that are sinuose and pitted throughout the leaf. In addition, their setae are longer (over 10 mm) and their capsules are cylindrical. In *H. pulchellum* the basal cells are commonly porose but the upper leaf cells are smooth-walled.

In Panama and Costa Rica plants of *H. pulchellum* are larger-sized in all features, the leaf margins just above the basal cells have a few sharp serrations and the upper leaf margins are at times widely and bluntly dentate. This expression of *H. pulchellum* is also found in Venezuela and Peru.

Breedlovea chiapensis, a recently described genus and species from Mexico, is gametophytically identical to the type expression of *H. pulchellum*. Sporophytically, the two taxa are nearly identical. They differ in that the peristome teeth of *B. chiapensis*, is papillose above but has papillae on the lower dorsal surface arranged in vertical rows while the peristome teeth of *H. pulchellum* are papillose throughout. Structurally, the peristome teeth of both taxa are the same i.e. inserted near the mouth, lanceolate, undivided, or irregularly fenestrate. In view of the overall closeness of these two taxa and the occurrence in *H. terebellatum* of a peristome similar to the *B. chiapensis* peristome, *Breedlovea chiapensis* and



Figures 1-11. *Holomitrium sinuosum*. Figure 1. Peristome teeth, outer (dorsal) surface. Figure 2. Sporophyte with perichaetial leaves. Figure 3. Upper marginal leaf cells. Figures 4, 8 & 9. Leaves. Figure 5. Leaf apex. Figure 6. Plant. Figure 7. Median leaf cells. Figure 10. Alar cells. Figure 11. Basal leaf cells. Scales for 1, 3-5, 7-11 in mm; scales for 2 & 6 in cm.

Holomitrium pulchellum are considered synonymous.

4. *Holomitrium sinuosum* Allen species nova

Species nova ab affinibus distincta; differt foliis crispatis, foliis cellulis porositis ubique, cellulisque superis rectangularibus.

Type. Panama. Bocas del Toro: vic. of Fortuna Dam, 2.8 miles along pipeline road leaving Chiriquí Grande road at Continental Divide, 8°55'N, 82°08'W, 850-950 m, Allen 5648 (MO holotype, PMA isotype).

Plants medium to large, tufted, greenish-yellow above, yellow-brown below, corticolous or humicolous. Stems erect, up to 5-7 cm long, branches few, irregular, simple. Leaves crowded, erect at base spreading above when wet, twisted and crispate above when dry, variably undulate on the margins, strongly concave to keeled. Leaves abruptly narrowed from an ovate base, broadly acuminate above, 8-10 mm long, apex acuminate, margins erect to incurved, crenulate below, serrate at extreme apex, unistratose throughout. Costae percurrent to shortly excurrent, smooth or weakly toothed at back. Upper laminal cells rectangular, incrassate, the outer and inner walls strongly sinuose, smooth, basal cells linear-rectangular, walls incrassate, pitted and sinuose, smooth, alar cells quadrate to rectangular, usually forming distinct, persistent groups of red-brown cells (occasionally the alar cells hyaline and more or less fugacious), cell walls usually firm. The leaf cells in the basal and upper regions grading imperceptibly into one another. Perichaetial leaves reaching the capsule middle. Setae 10-15 mm long, yellow. Capsules erect to weakly curved above, cylindrical, 2.5-3.0 mm long, brown. Stomata phaneropore. Peristome reddish orange, teeth linear-lanceolate, densely papillose, 0.6-0.7 mm high. Opercula 2.5

mm long. Calyptrae 4.5 mm long.

Illustrations. Figs. 1-11.

Distribution. Costa Rica (Alajuela, Puntarenas, San José); Panama (Bocas del Toro, Chiriquí, Cocle, Panama); Venezuela (Amazonas); Colombia (Antioquia).

Habitat. Corticolous on trunks and branches, humicolous on roots of epiphytic plants and over humus along roadsides; 700-2920 m.

Specimens examined. COSTA RICA. Alajuela: La Palma de San Ramón, Brenes 16213c, 16218b (all NY); Puntarenas: Monte Verde reserve, 10°19'N, 84°43'W, Hammel et al. 15389 (MO); San José: vic. of La Palma on road to La Hondura, Maxon & Harvey 7982 (NY, US). PANAMA. Bocas del Toro: vic of Fortuna Dam, 2.8 mi along pipeline road leaving Chiriquí Grande at Continental divide, Allen 5597, 5648 (all MO), Cerro Colorado, ca 7 mi from Chami Camp, McPherson 8850D (MO); Chiriquí: slopes not of Fortuna Dam lake, Allen 5434, 5441, 5454B, 5458, 5467, 5503, 5506A (all MO); Cocle: Alto Calvario, 7 km north of El Cope, Folsom & Collins 6476 (MO); Panama: Cerro Campana, 8°40'N, 79°55'W, Crosby 4365 (MO), near summit Cerro Campana, Croat 22801 (MO). VENEZUELA. Amazonas: Dept. Atabapo, Cerro Marahuaca, summit of SE corner, 3°37'N, 65°21'W, Liesner 24787 (MO). COLOMBIA. Antioquia: Municipio de Belmira, NE de Belmira, 6°33'N, 75°40'W, Churchill et al. 15600 (MO, NY).

Holomitrium sinuosum is a robust species with leaves that are crispate above, undulate on the margins and spreading from the insertion. The most distinctive feature of this species is the presence of strongly porose cells throughout the leaf. Unlike most *Holomitrium* species the upper leaf cells are rectangular, not quadrate, and they grade smoothly into the cells in the basal region of the leaf. The leaves are broadly ovate, but non-clasping, at base, and the leaf margins are essentially crenulate except for a few serrations at the apex. The alar cells are remarkably variable in this species. Mostly they are red-brown and persistent, however, at times leaves from the same stem will have alar cells that

are hyaline and fugacious.

This species is close to *H. terebellatum*. In both species the upper leaf cells are elongated with sinuose outer cell walls, and they have the same size and habit. More importantly, in *H. terebellatum* the cellular differentiation between the basal and upper regions of the leaves is very weak. *Holomitrium sinuosum* can be distinguished on the basis of the broadly ovate leaf bases, longer leaf cells with both the outer cell walls and cell lumens strongly sinuose, crenulate lower leaf margins, and the presence of persistent as well as fugacious alar cells. In contrast, the leaves of *H. terebellatum* are oblong at base, the leaf cells are irregularly rectangular to nearly quadrate, commonly only the outer cell walls are sinuose, the leaf margins are sharply serrate, and the alar cells are fugacious. The South American *H. flexuosum* is also similar to *H. sinuosum* and *H. terebellatum*. *Holomitrium flexuosum*, however, has quadrate upper leaf cells with straight cell walls.

Holomitrium sinuosum may be confused with *Schliephackea meteoroides* or *Eucamptodontopsis brittonae* since all three species have upper cells that are not sharply differentiated from the basal cells. In *S. meteoroides*, however, the leaves are sharply serrate throughout and in *E. brittonae* the leaves are spirally contorted, crenulate throughout and the upper leaf cells linear-rectangular.

5. *Holomitrium terebellatum* C. Müll. in Ren. & Card., Bull. Soc. Roy. Bot. Belgique 31: 151. 1893. Type. Costa Rica, Forêts du Barba, Tonduz, Pittier 5518 (NY isotype).

Plants medium to large, tufted, green to yellowish-green above, yellowish-brown below, corticolous. Stems erect, 3-6 cm long, branches few, irregular, simple. Leaves crowded, evenly spaced, erect-spreading, when wet, crisped and strongly contorted when dry, keeled above, concave

below, leaves generally spreading from the insertion, not or weakly clasping at base, oblong below, gradually narrowed and linear-lanceolate above, 7-9 mm long, apex narrowly acuminate, margins erect, serrate to denticulate from midleaf to the apex, uni-stratose. Costae excurrent, toothed at back near apex. Upper laminal cells rounded-rectangular to irregularly quadrate, walls incrassate and sinuose, smooth, basal cells strongly differentiated, linear, yellowish, walls incrassate, pitted, smooth, those at the margins narrower than the interior cells, incrassate and pitted, alar cells differentiated but commonly fugacious, hyaline, thin-walled. Perichaetial leaves reaching to the base of the capsule. Setae 10-20 mm long, yellow. Capsules erect, cylindrical, 2-3 mm long, brown. Stomata phaneropore. Peristome undivided, hyaline above reddish below, teeth linear-lanceolate, densely papillose above the papillose in more or less vertical lines below, 0.5 mm high. Opercula 2.5 mm long.

Illustrations. Bartram (1949, Fig. 27, A-C).

Distribution in Central America. Costa Rica (Alajuela, Cartago, Heredia, Limón, Puntarenas, San José); Panama (Chiriquí).

Habitat. Corticolous on trunks and branches, rarely terrestrial; 1400-2500 m.

Specimens examined. COSTA RICA. Alajuela: La Palma de San Ramon, Brenes 11465 (NY); Cartago: El Mumece on the Río Navarro, Standley & Torres 50911 (NY, US), vic. of Orosi, Standley 39849 (US); Heredia: northeast of San Isidro, Standley & Valerio 50101, 50525 (all US), Cerro de las Caricias north of San Isidro, Standley & Valerio 52213 (NY, US), El Gallito, Valerio 114 (US), Volcán de Barba, Valerio 13 (US), forêts de Barba, Tonduz (NY); Limón: Cordillera de Talamanca, 9°08'N, 82°57'W, Davidse et al. 28775, 28975 (MO); Puntarenas: 5 km S of Vito, 8°45'N, 82°59'W, Crosby 2645 (MO), Monte Verde, Crosby 2520 (MO); San José: SE slopes of Cerros de Zurqui, 10°03'N, 84°01'W, Crosby & Crosby 8596 (MO), Zurqui, Standley & Valerio 48261 (US). PANAMA: Chiriquí: upper Caldera River, Holcomb's trail above El Boquete, Maxon 5696 (US).

Holomitrium terebellatum is one of the largest species of *Holomitrium* in Central America. It is recognized by the following combination of character states: robust size with leaves generally spreading from the insertion; serrate leaf margins; rounded-rectangular to irregularly quadrate upper leaf cells with sinuose outer walls; and fugacious alar cells. The fugacious alar cells of *H. terebellatum* are a distinctive feature of the species. Commonly, nothing remains of the alar region except the topmost row of cells and a rounded gap. In Central America the alar cells of both *H. pulchellum* and *H. sinuosum* may be fugacious. These species differ from *H. terebellatum* in having subentire to crenulate leaf margins. In addition, *Holomitrium pulchellum* is a smaller plant with quadrate, straight-walled upper leaf cells. In *H. sinuosum* the leaves are broadly ovate at base, the upper leaf cells have strongly sinuose cells walls as well as cell lumens and the alar cells are more commonly persistent.

Holomitrium terebellatum is very close to the South American *H. flexuosum*. The two species differ only in the straight-walled upper leaf cells and persistent alar cells of *H. flexuosum*.

6. *Holomitrium williamsii* Bartr., Contr. U.S. Natl. Herb. 26: 67. 1928. Type. Costa Rica, Yerba Buena, northeast of San Isidro, *Standley & Valerio 49939* (F, US).

Plants medium sized, densely tufted, greenish-yellow above, yellowish-brown below, corticolous. Stems erect, 2-3 cm long, branches few, irregular, simple. Leaves crowded, erect-spreading when wet, strongly crisped when dry, keeled above; leaves oblong-ovate, clasping at base, abruptly narrowed to the linear-lanceolate upper leaf, 4-5 mm long, apex acute, margins plane, serrulate to dentate in the upper two-thirds, irregularly bistratose at the margins and in patches

throughout the lamina. Costa dorsally toothed above. Upper leaf cells rounded-quadrate, homogeneous, walls evenly thick-walled, basal leaf cells linear, yellowish, the walls incrassate and pitted, those at the basal margins narrower than the interior cells and porose, alar cells well-developed, persistent, reddish-brown, hyaline near the costa. Commonly with clusters of deciduous, flagellate branches at the apex of the stem; leaves short, broadly ovate, obtuse to minutely apiculate, ecostate, closely appressed-imbriated. Sporophytes not known.

Illustrations. Bartram (1928, Fig. 10, A-H).

Distribution in Central America. Costa Rica (Heredia); Panama (Darién).

Habitat. On tree trunks; 1850-2000 m.

Specimens examined. COSTA RICA. Heredia: Yerba Buena, *Standley & Valerio 49939* (NY, US), Volcán Barba, *Hatheway & Hatheway 1713A* (US). PANAMA. Darién: Cerro Tacarcuna, *Mori & Gentry 4431* (MO).

Holomitrium williamsii is best recognized by its apical clusters of flagellate branches; it is the only Central American species with such structures. When flagellate branches are absent the species can be confused with *H. arboreum*, since the two species have leaves with the same size and shape. The presence along the upper basal leaf margins of elongate, narrow, and porose cells instead of quadrate cells separates this species from *H. arboreum*.

Holomitrium williamsii appears to be closely allied to the Caribbean species *H. calycinum*. These species share a number of features: 1. irregularly bistratose leaf margins and laminae, 2. elongate and narrow basal marginal cells, 3. an abrupt basal to median laminal cell transition and 4. deciduous flagellate branches. But, in *H. calycinum* the leaves are more abruptly narrowed above, the upper leaf limb is

more linear and the leaves of the flagellate branches have percurrent costae.

Florschütz (1964) in reporting *H. williamsii* from Surinam and Guyana described its sporophyte for the first time. However, one of the specimens he cited (*Rombouts s.n.*, MO) is identical in both its gametophyte and sporophyte to *H. antennatum*, a species allied to *H. arboreum* rather than *H. calycinum*.

Excluded Species.

1. *Holomitrium calycinum* (Hedw.) Mitt.

This species typically has leaves with either bistratose margins or bistratose regions in the leaves. This feature is also found to varying degrees in *H. arboreum* and *H. williamsii*. All collections of *H. calycinum* reported from Central America have been found to be either *H. arboreum* or *H. williamsii*.

2. *Holomitrium crispulum* Mart.

The single reported collection of *H. crispulum* from Central America (*Williams 1059*, NY), from Panama) is actually *H. arboreum*. *Holomitrium crispulum* and *H. arboreum* are in fact closely related in that the leaves of both species have upper quadrate cells that extend downward along the basal leaf margins. But, the leaf laminae of *H. crispulum* have extensive areas of bistratose cells while in *H. arboreum* the leaves are generally unistratose or irregularly bistratose only along the margins.

3. *Holomitrium falcatum* Bartr.

Hegewald (1977) was the first to synonymize this species with *Dicranum flagellare*. An examination of type material re- confirms this decision.

4. *Holomitrium flexuosum* Mitt.

This South American species has been reported from Guatemala (*Standley 81822*) and Costa Rica (*Brenes 16218b & Valerio 471*). The Guatemalan report, as noted by Hegewald (1977), is *Dicranum flagellare*.

The Brenes collection is *Holomitrium sinuosum*. I have not seen the Valerio collection. *Holomitrium flexuosum* is very close to *H. terebellatum* and *H. sinuosum* in plant size, leaf shape and areolation. However, it differs from those two species in having quadrate, straight-walled upper leaf cells rather than rectangular, sinuose-walled cells.

3. *Schliephackea* C. Müll., Flora 58: 532. 1875.

Type species: *S. prostrata* C. Müll.

Plants medium to large sized, in long pendant tufts. Stems reddish-brown, central strand present. Leaves linear-lanceolate from a widely spreading base, margins erect, serrate; costa single and strong; alar cells well developed, leaf cells elongate-rectangular to linear, incrassate and variously porose throughout. Pseudautoicous. Perichaetial leaves sheathing at base, long setaceous above. Capsule erect, peristome teeth undivided. Calyptra cucullate.

There are three features that mark *Schliephackea*: 1. a pendant habit, 2. leaf cells elongate, and porose throughout, the upper and lower cells grading into one another and, 3. sharply serrate leaf margins. Within the *Holomitrium*-complex only the pendant habit is unique to *Schliephackea*, however, the combination of the other two features is not found in any other species of the complex. There are two species of *Schliephackea*, only one of which occurs in Central America.

Key to the species of *Schliephackea*

1. Leaves linear, evenly tapered throughout, long setaceous above; loosely spirally twisted from the base when dry, upper leaf cells linear, weakly porose

.....*S. prostrata* (Colombia, Ecuador)

1. Leaves lanceolate from an ovate base, narrowly acuminate above; flexuous or tightly spirally twisted above when dry; upper leaf cells rounded-rectangular, strongly porose

..... *S. meteoroides* (Costa Rica, Panama, Colombia)

***Schliephackea meteoroides* (Williams)**

Broth. Nat. Pflanzenfam. 10: 207. 1924. *Dicranoloma meteoroides* Williams, Contr. U.S. Natl. Herb. 16: 23. 1912. Types: Panama, Chiriquí between Alto de las Palmas and top of Cerro de la Horqueta, Maxon 5499. (NY holotype, US isotype); Pittier 7005 (NY, US paratypes).

Plants medium to large sized, in lax pendant tufts, greenish-yellow, corticolous. Stems pendant from branches and shrubs, up to 30 cm long, branches few, irregular, simple, central strand small. Leaves distant, more or less ranked, spreading at right angles to flexuous from a broadly ovate base when wet, undulate below and spirally twisted above, when dry; leaves lanceolate from an ovate base, 7-10 mm long, apex slenderly acuminate, margins erect to incurved, keeled above, serrulate in the upper 3/4. Costa single, shortly excurrent, smooth throughout. Upper laminal cells rounded-rectangular (at times elongate-rectangular or rarely subquadrate), irregularly quadrate at the margins, walls incrassate, pitted and sinuose; basal cells linear-rectangular, walls incrassate and pitted; alar cells strongly differentiated, red-brown, walls thickened. Pseudautoicous. Perigonia on dwarf males growing on tomentum of female plants. Perichaetia at stem apex, strongly differentiated, perichaetial leaves sheathing at base, long setaceous above and reaching up to beyond the capsule.

exserted, erect, cylindrical, 2.5 mm long, brown. Exothecial stomata phaneropore. Peristome teeth undivided, orange-red, lanceolate ending in a long, fine, hyaline point, papillose, 0.5-0.6 μm high. Opercula subulate rostrate, 2.0-2.5 mm long. Calyptrae cucullate, 2.5 mm long.

Illustrations. None.

Distribution in Central America. Costa Rica (Alajuela, Heredia, San José); Panama (Bocas del Toro, Chiriquí, Cocle, Panama).

Habitat. Hanging pendant from branches of trees and shrubs; 700- 2600 m.

Specimens examined. COSTARICA. Alajuela: Los Angeles de San Ramón, Brenes 16253 (F, NY), San Ramón, Piedades Sur y La Palma, Brenes 16215 (F); Heredia: Laguna Barba, 10°05'N, 83°55'W, Crosby 10939 (MO), Cerros de Zurquí, Standley & Valerio 50516 (NY, US), 10°03'N, 84°01'W, Crosby 10874 (MO), Cerro de Las Lajas, Standley & Valerio 51601, 51606 (both F, NY), Cerro de las Caricias, Standley & Valerio 52171 (NY, US), Las Vueltas, 10°06'N, 84°03'W, Crosby & Crosby 6049, 6421, 6560, 93330 (MO), Crosby 9880 (MO), between San Rafael and Río Las Vueltas, 10°05'N, 84°04'W, Stevens 13965 (MO); San José: 17 km SE of El Empalme, 9°37'N, 83°48'W, Crosby 10952 (MO), La Hondura, Standley & Valerio 51811 (NY, US). PANAMA. Bocas del Toro: Cerro Colorado, ca 3-12 mi above Camp Chami, Allen 5126, 5182, 5311 (all MO); Fortuna Dam, along Continental Divide trail, Allen 5698, 5715, 5731, 5746 (all MO), McPherson 9030A (MO), trail from Boquete to Cerro Pate Macho and into Bocas, McPherson 8314A (MO); Chiriquí: Alto de las Palmas and top of Cerro Horqueta, Maxon 5499 (NY, US), Pittier 7005 (NY, US), Cordillera, east of Río Caldera, Killip 5329 (NY, US), Killip 5312 (US), Fortuna Dam, Allen 5489, 5455, 5505 (all MO), Holtum trail to Cerro Horqueta, Crosby 4069 (MO); Cerro Colorado, Luer et al. 10542 (MO); Cocle: above Cope, ca 8°38'N, 80°35'W, McPherson 7694E (MO), summit Cerro Pilon, N of El Valle de Anton, 8°35'N, 80°10'W, Crosby 4440 (MO, NY); Panama: Cerro Campana, 8°40'N, 79°55'W, Crosby 10073 (MO).

The pendant habit of *S. meteoroides* is a remarkable feature that helps in recognizing the species. Commonly the plants appear to be draped over upper twigs and branches with a minimal amount

of rhizoidal attachment. *Schliephackea meteoroides* is distressingly variable in most of its features. Typically the widely spaced leaves are flexuous above and strongly spreading to almost circinate from a broadly ovate base. But, many collections can be found with leaves simply spreading from an ovate base and spirally contorted above. The leaf cells are commonly rectangular and porose throughout and the leaf margins are sharply serrate. However, the leaf cells can vary from subquadrate to elongate-rectangular and from smooth-walled to strongly porose. The leaf margins can at times be weakly serrate and distinctly undulate when dry.

This species can easily be confused with several members of the *Holomitrium*-complex. From *Eucamptodontopsis brittonae* and *Holomitrium sinuosum*, *Schliephackea meteoroides* is distinguished by its serrate leaf margins (irregularly crenulate below in first two). From *H. terebellatum* it is best separated by its persistent alar cells (fugacious in *H. terebellatum*). When found in the expression characterized by spirally contorted leaves, weakly serrate leaf margins and leaf cells subquadrate and smooth walled, *S. meteoroides* is nearly identical to *H. flexuosum*. In this expression of *S. meteoroides* the two species differ only in the pendant habit and widely spaced leaves of *S. meteoroides*. In *H. flexuosum* the plants are erect and the leaves are more closely spaced.

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