Introduction

Central America has one of the most diverse moss floras in the world. Its 871 species are found in an area three-fourths the size of Texas. Indeed, it has roughly the same number of mosses as Colombia, which is nearly twice as large. There are several factors responsible for this remarkable diversity. Central America is a tropical region with a diverse landscape marked by great vertical relief. Thus, the region provides a broad range of habitats in a small area. Central America also has an eclectic moss flora that has benefited from its physical closeness to three distinct and diverse species-source areas: South America, North America and the Caribbean.

The Central American region is treated here as a political unit extending from the southern border of Mexico eastward and southward to the northern border of Colombia. The area includes seven countries, Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama. This region stretches from latitude 7o to 19o N with a longitudinal axis running northwest to southeast for 1,800 km. The total area encompassed is 522,765 km2.

Parts of at least three tectonic plates (North American, Caribbean, and Nazca plates) have contributed to the Central American land mass, and because of this the region is geologically complex. Nevertheless, it can be grossly divided in two: a northern part, continental in character, including Guatemala, Belize, Honduras, El Salvador and northern Nicaragua, and a southern part, oceanic in origin, consisting of southern Nicaragua to Panama. The southern part now occupies an intermediate position between a purely oceanic and a purely continental crust. One of the most distinctive geological features of Central America is the Nicaraguan Depression, thought to mark the boundary between the northern and southern parts of Central America. This depression runs from the northern Caribbean coast of Costa Rica through southwestern Nicaragua. Much of the Nicaraguan Depression is occupied by Lake Managua and Lake Nicaragua.

Central America is a region of pronounced vertical relief. To the north the mountains form an arc extending from southwestern Guatemala through northern Honduras and into northern Nicaragua. These northern sierras consist of several parallel mountain chains separated by faults and grabens. The sierras of southern Central America begin as low-altitude ranges on the Pacific coast of Nicaragua and
extend through Costa Rica and Panama. Below the northern sierras (central Nicaragua, southwestern Honduras, and parts of El Salvador) are large areas of tertiary volcanic ranges and plateaus, and a narrow chain of quaternary volcanoes, some still active, occurs along the Pacific side of the region.

The quaternary volcanic chain is nearly continuous from the Mexican border to northern Costa Rica and extends sporadically from southern Costa Rica through Panama. It is paralleled, in the Pacific Ocean, by the Middle American Trench. This chain of volcanoes is thought to be causally related to active subduction of the Cocos Plate below the North American and Caribbean plates.

The northern edge of Central America (Peten region of Guatemala and Belize) consists of low-lying areas of extensive limestone formations. This region forms tablelands in the north and in the south merges via chains of folded mountains with the sierras of Guatemala. Major areas of coastal plains are found in eastern Belize, western Guatemala, eastern Honduras (Mosquitia embayment), eastern Nicaragua (Caribbean coastal plain), and northeastern Costa Rica (Limon basin).

Endemism in Central American mosses appears to be low. Only 10% (20 out of 203) of the species treated in Part 1 of the Moss Flora of Central America are endemic. Since Central America is a region that connects two continental masses that have basically different moss floras – Laurasian North America with a strong Hypnobyalean component and Gondwanalandian South America with a strong Isobryalean component – the region is likely to be phytogeographically complex. At present a definitive statement on the phytogeographic relationships of Central American mosses cannot be made because only the first fourth of the mosses have been treated in detail. Several broad patterns, however, are evident.

Most Central American mosses belong to a northern neotropical flora that extends from southern Mexico, through Central America, Colombia, Venezuela, the Guianas, Ecuador, and parts of Peru and Brazil. Central American mosses are an integral part of the northern neotropical flora. A closely allied but extremely rare element of the Central American flora is that part whose affinities are with the Guayana Highlands of South America. An outstanding example of this pattern is the presence of Octoblepharum tatei in the mountains of northeastern Honduras.

The second largest phytogeographic element in the Central American moss flora has
north temperate affinities. This element of the flora is best represented in northern Central America and includes such species as Sphagnum imbricatum, Andreaea alpestris, Blindia acuta, Fissidens dubius, Trematodon longicollis, Anisothecium rufescens, and Dicranum flagellare. A subset of this northern element consists of species whose affinities are with those of northern Mexico and the southwestern region of the United States. Dicranum rhabdocarpum exemplifies this type of pattern.

Another relatively large element in the flora is made up of species more commonly found in the Caribbean region. This Caribbean element is found in the southeastern United States, eastern Mexico, the Caribbean islands, low-lying areas of the Guianas, and southeastern Brazil. The Caribbean element in Central America is most common in Belize, northern Guatemala, and northeastern Nicaragua. Species with this type of distribution include Sphagnum portoricense, Campylopus angustirietis, Leucoloma mariei, Hookeriopsis websteri, Fissidens weirii var. insertus, Dicranella harrisii, Leucobryum incurvifolium, Octoblepharum cylindricum, and many members of the Calymperaceae.

There is a small number of Central American mosses that are also found in Africa. These, however, do not represent a discrete floristic element but rather a relationship between the African mosses and the northern neotropical flora. At present the number of species with this type of distribution is small, but it will surely increase as the African flora becomes better known. Central American mosses with this distribution include Campylopus nivalis, Ochrobryum gardneri, Leucophanes molleri, and Syrrhopodon cryptocarpos.

South temperate floristic elements are occasionally found in Central America. Andreaea subulata is an example of a south temperate species that reaches its northernmost limit in Honduras. It is otherwise known from southeastern Australia, New Zealand, South Africa, and Patagonia, with isolated mountain stations in Borneo, eastern Africa, and the Andes of Colombia and Bolivia. A somewhat similar distribution pattern is shown by Tristichium mirabile and Aongstroemia julacea, which are present at high elevations in Costa Rica as well as isolated mountain stations throughout the Southern Hemisphere.

Garckea flexuosa is a common and weedy Asian species known in Central America from a single Panamanian locality. Its occurrence in Central America may be
The Moss Flora of Central America attempts to treat all mosses known or reported from the region. It is specimen-based, and wherever possible type specimens have been examined. Type information is given for all species. However, not all type material has been examined. Examination of type material is indicated within the text by the citation of an Index Herbariorum, Ed. 8 acronym at the end of the type information.

The families will be treated sequentially in roughly the same phylogenetic sequence as Bartram's Mosses of Guatemala (1949). As much as possible the generic keys and descriptions refer to the genera as a whole not just to the species found in Central America. To facilitate use, the genera are arranged alphabetically within the families and the species alphabetically within genera. There is one exception to this arrangement: Sphagnum species are arranged alphabetically under their sections.

Generic and species descriptions are short, emphasizing only features critical for recognition. For each species a list of previously published illustrations is given. Short, concise habitat notes based on my field experience with the species or taken from specimen labels follow the citation of illustrations. The distribution of all species is determined by the examination of specimens. All species for which a specimen cannot be located are placed in a "Species Excluded" section. The distribution of species within each country is documented by the citation of one specimen from each political unit, department or province, in which the species occurs.

An indication of the world range of each species, based on an examination of specimens or extracted from reliable literature reports, is given. With two exceptions, the system put forward by the World Geographical Scheme for Recording Plant Distributions (Hollis & Brummitt, 1992), at the continental and regional levels, is used for world ranges. Within the citations only the regional groups are named, and they are arranged into continental groups that are set off from each other by semicolons. Here all of Mexico and Central America, as defined above, are treated as continental regions, set off by semicolons. Hollis and Brummitt divide Mexico between their Northern and Southern American continents and treat Central America as part of Southern America.

Acknowledgments

National Science Foundation grant BSR-8700420 to the Missouri Botanical Garden financially supported work on the Moss Flora of Central America. National Geographic Society grants 3165-85 and 4058-89 to Gordon McPherson and 4556-91 to Gerrit Davidse supported fieldwork in Panama and Honduras. Peter H. Raven is gratefully...
acknowledged for his unqualified support and commitment to this project as well as to
muscology at the Missouri Botanical Garden.

I thank William R. Buck (NY) for carefully reading and commenting on early drafts
of this Flora. The Flora has benefited greatly from the expertise of Robert E. Magill
(MO). I thank Jan-Peter Frahm (DUIS) for his views on Campylopus and
Dicranodontium, Barbara M. Murray (ALA) for comments on Andreaea, and Jerry A.
Snider (CINC) for help with Ditrichaceae. Harold Robinson (US) provided stimulating
discussions on the Holomitrium-complex and on the Leucobryaceae. The illustrations of
Sphagnum compactum and S. macrophyllum are reproduced by permission of The New
York Botanical Garden. Finally, I thank Barb Mack (MO) for correcting and formatting
the word-processed files from which this book was produced.

SPHAGNACEAE

by Howard Crum

Plants of wet places, sometimes submerged but more commonly above water level,
in carpets, cushions, or hummocks; stems sparsely forked, consisting of a central
parenchyma surrounded by a wood cylinder of thick-walled prosenchyma enclosed by a
cortex of 1 or more layers of large, empty hyaline cells; rhizoids restricted to the base
of young gametophores, with oblique cross-walls. Stem leaves less crowded, usually
differentiated in size, shape, and structure, the hyaline cells often divided, generally
with a poor development of pores and fibrils but usually extensively resorbed on 1 or
both surfaces and showing membrane pleats or irregular membrane gaps. Branches in
fascicles spirally disposed around the stem and crowded at the stem tip in a headlike
tuft, or capitulum, some branches spreading to ascending, others more slender and
pendent; branch cortex usually of 1 layer of hyaline cells, often with some cells
differentiated as enlarged, apically porose retort cells. Branch leaves arranged in 5
rows, sometimes conspicuously so, commonly bordered by a few rows of linear cells,
otherwise consisting of a network of narrow green cells enclosing large, empty hyaline
cells nearly always reinforced by ringlike fibrils and porose at the surface. Antheridial
branches catkinlike, with leaves commonly crowded in spiral rows and often highly
colored, the antheridia globose and long-stalked, borne singly beside each leaf of the
catkin. Perichaetial branches short, bearing 1-5 flask-shaped archegonia at the apex,
the perichaetial leaves much larger and otherwise differentiated from stem and branch
leaves, enclosing the sporophyte until its maturity. Sporophyte consisting of a globose
capsule and a massive foot embedded in the tip of the perichaetial branch, which
elongates to elevate the mature capsule beyond the perichaetium; capsules eperistomate,
operculate, the wall of the urn of several cell layers with no intercellular spaces, usually
bearing in the lower half or more a large number of pseudostomata sunken beneath the
surface and consisting of paired guard cells but no pore; columella domelike,
surrounded and overarched by large, tetrahedral spores. Calyptrae of a delicate, hyaline
membrane irregularly ruptured as the capsule nears maturity. Protonemata thallose,
producing 1 or rarely 2 leafy gametophores, also proliferating secondary protonemata at
the ends of marginal, filamentous outgrowths.

The family consists of a single genus.

1. 

Sphagnum L., Sp. Pl. 1106. 1753.

Key to the Sections of Sphagnum

1. Cortical cells of stems and branches generally reinforced by delicate spiral fibrils;
branch leaves broad, cucullate-concave, rough at back of the apex, and denticulate
along a marginal resorption furrow

1. Sphagnum sect. Sphagnum

1. Cortical cells not fibrillose; branch leaves narrower and generally tapered to a
slender, involute-concave tip, not cucullate or roughened at the apex and only rarely
toothed at the sides or bordered by a resorption furrow

2. Branch cortical cells uniformly porose at their upper ends; stem leaves very small; branch leaves broadly truncate, denticulate at the margins along a resorption furrow

2. Sphagnum sect. Rigida

2. Branch cortical cells of 2 kinds, some without pores, others large, apically porose and retort-shaped; stem leaves generally not particularly small; branch leaves tapered to a narrow, truncate apex, not denticulate, bordered by linear cells in 2 or more rows

3. Plants aquatic; branch leaves with hyaline cells very long, not much broader than the green cells, without fibrils but with many pores on the outer surface (8-20 in 1 row or 15-60 in 2 rows)

3. Sphagnum sect. Isocladus

3. Plants mostly not aquatic; branch leaves with hyaline cells distinctly broader than green cells, fibrillose, usually with no more than 8 pores on the outer surface

4. Plants usually orange-yellow tinged; branches of the capitulum (at least) usually curved; branch leaves usually more or less secund; pores of hyaline cells of branch leaves usually crowded in beadlike rows along the commissures on 1 or both surfaces (S. trirameum has slenderly tapered branches and few pores)

4. Sphagnum sect. Subsecunda

4. Plants green, yellowish brown, pink, or red; branches not or rarely curved; branch leaves erect or spreading, not or rarely more or less secund; pores of
hyaline cells fewer, not crowded in commissural rows

5. Plants commonly red or red-tinged; green cells of branch leaves almost always exposed more broadly on the inner surface
   6. Sphagnum sect. Acutifolia

5. Plants not reddish; green cells exposed more broadly on the outer surface (See also S. trirameum)
   4. Sphagnum sect. Cuspidata

1. Sphagnum sect. Sphagnum
   1. Green cells of branch leaves equilateral-triangular in section, the hyaline cells adjacent to them with fringe fibrils on their side walls (usually conspicuous, at least at leaf bases)
   2

2. Branches club-shaped; cortical cells of branches funnel-shaped and nested together, not porose at the surface
   4. S. portoricense

2. Branches not club-shaped; cortical cells of branches not funnel-shaped, with few to many pores at the surface
   1. S. imbricatum

3. Plants usually red or pink; branch leaves, on the outer surface, with elliptic, ringed pores; green cells central and entirely included and hyaline cells plane on both surfaces
   2. S. magellanicum

3. Plants brown, yellow-brown, or orange; branch leaves with elliptic, ringed pseudopores; green cells narrowly triangular to lenticular, more or less equally
exposed, and hyaline cells convex on both surfaces

3. S. perichaetiale

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1. Sphagnum imbricatum

2. Sphagnum magellanicum


Plants often fairly robust, in pale green to dark yellow-brown cushions, hummocks, or carpets; cortical cells in 3-4 layers, fibrillose, the outer cells with few to many irregularly rounded pores, the inner walls of the innermost cells finely cross-striate; wood cylinder of stem brown. Stem leaves oblong to lingulate, rounded at the apex, finely fringed and hyaline at the margins; hyaline cells commonly divided, without fibrils and pores, almost entirely resorbed on the outer surface. Branches stout, normally in fascicles of 5 (2 spreading), cortical cells in 1 layer, fibrillose, 1(-2)-porose, the inner walls finely cross-striate. Branch leaves broadly ovate, cucullate-concave, roughened at back of the apex and serrulate-bordered by a resorption furrow;
hyaline cells very concave on the outer surface, nearly plane on the inner, on the outer surface with 2-5 large, ringed, elliptic pores, in 3's at adjacent angles, more numerous (11-17) and rounded-elliptic toward the middle of the leaf base, on the inner surface toward the leaf apex with small, ringed corner pores and also 1-6 very large, round, unringed pores in a single row or, toward the margins, as many as 12 in 2 rows; green cells in section equilateral-triangular, broadly exposed on the inner surface, the side walls of hyaline cells beset with comb fibrils (often present only near the leaf insertion).

Illustrations. Crum (1980, Fig. C); Crum and Anderson (1981, Fig. 4); Crum (1984, Fig. 7).

Distribution in Central America. BELIZE. Cayo: Mains 4105 (MICH, NY).

World range: Subarctic America, Western and Eastern Canada, Northwestern, North-Central, Northeastern, South-Central, and Southeastern U.S.A.; Central America; Caribbean; Northern, Southwestern, Middle, East, and Southeastern Europe; Caucasus, Soviet Far East, Eastern Asia.

This species is known by its branch leaves with green cells broadly triangular in section and adjacent hyaline cell walls ornamented by comb fibrils. The comb fibrils are sometimes conspicuous and at other times scarcely developed, but they can usually be detected at the leaf insertions.

Flatberg (1984) has referred the Belize material, as well as collections from Guatemala and Cuba, to subsp. affine (Ren. & Card.) Flatb., but I see no reason to subdivide the species in its more inclusive, traditional sense.

Plants stout, in dense, pink, red, or purplish (green if shaded) cushions or hummocks; cortical cells in 3-4 layers, the outermost cells delicately spiral-fibrillose, with 1 (or occasionally 2-4) large, round to elliptic pores; wood cylinder red. Stem leaves more or less flat, oblong-lingulate, rounded at the apex and finely fringed at the margins; hyaline cells not divided, fibrillose near the leaf apex or not at all, largely resolved on the outer surface, sometimes on both surfaces. Branches stout and tumid, in fascicles of 4-5 (2 spreading); cortical cells fibrillose, sometimes with 1 large, round pore near the upper ends. Branch leaves imbricate or rarely somewhat spreading at the tips, ca. 2 mm long, broadly ovate, deeply cucullate-concave, rough at back of the apex and denticulate along a marginal resorption furrow; hyaline cells plane or nearly so on both surfaces, on the outer surface with 2-5(-10) large, elliptic, ringed pores at ends, corners, and commissures, usually in 3's at adjacent cell angles, on the inner surface with 0-5 round to elliptic pores or pseudopores at corners and commissures in upper and side regions; green cells in section small, elliptic, central and entirely included.

Illustrations. Crum (1980, Fig. A); Crum and Anderson (1981, Fig. 1 A-G); Crum (1984, Fig. 1).

Habitat. At moderate or (more commonly) high elevations, usually 2300-3900 m, rarely as low as 1000 m.

Distribution in Central America. GUATEMALA. Huehuetenango: Steyermark 49921 (NY). HONDURAS. Lempira: Allen 11497 (MICH, MO, TEFH); Olancho: Allen 12619 (MICH, MO, TEFH). NICARAGUA. Jinotega: Moreno 7804 (MO). COSTA RICA. Alajuela: Richards 6234 (MICH); Cartago: Crosby & Crosby 5763 (MO); Limon: Davidse & Herrera 29311 (MO); Puntarenas: Davidse et al. 26099 (MO); San Jose: Crosby & Crosby 5735 (MO). PANAMA. Bocas del Toro: Gomez et al. 22577 (MICH); Cocle: McPherson 11244 (MO); Darien: Mori & Gentry 4353 (MO); Veraguas: Mori 7604 (MO).

World range: Subarctic America, Western and Eastern Canada, Northwestern, North-Central, Northeastern, Southwestern, South-Central, and Southeastern U.S.A.; Mexico; Central America; Caribbean, Western, Northern, and Southern South America, Brazil; Northern, Southwestern, Middle, East and Southeastern Europe; Caucasus, Soviet Middle Asia, Siberia, Soviet Far East, Mongolia, China, Eastern Asia.

Sphagnum magellanicum normally grows exposed to the sun and develops a reddish color in response to insolation. It has cortical cells of stems and branches delicately fibrillose. The branch leaves have hyaline cells flat on both surfaces and green cells, in
section, central and entirely included.

The branch leaves of *S. alegrense* Warnst. have fine, vermiform ridges on the walls of the hyaline cells where they lie adjacent to green cells, and the cortical cells of stems and branches essentially lack fibrils. The species is known from Brazil, Venezuela, Guadeloupe, and Dominica. A report from Panama (Allen 1986) can be referred to *S. perichaetiale*.


Plants in rather small, dense, rounded clumps, soft, pale orange-brown or green tinged with red or pink; capitulum rounded in profile; cortical cells in 3-4 layers, those of the epidermis with 1-3 (rarely 6-8) pores and fibrils few and delicate or none; wood cylinder brown to dark purplish red. Stem leaves lingulate, rounded at the apex, finely fringed all around, generally approaching branch leaves in fibrils, pores, and membrane gaps. Branches in fascicles of 4-5 (2 spreading); cortical cells porose at their upper ends,
with fibrils very delicate or, more often, lacking. Branch leaves ovate, broadly pointed, and concave-cucullate, roughened at back of the apex and denticulate along a marginal resorption furrow; hyaline cells convex on both surfaces, on the outer surface with few inconspicuous pseudopores in 2's and 3's at adjacent corners, passing into irregular membrane gaps above, on the inner surface with few large, unringed pores at corners and commissures; green cells in section narrowly rectangular or lenticular, equally exposed on both surfaces.

Illustrations. Crum (1980, Fig. D); Crum and Anderson (1981, Fig. 1 O-T); Crum (1984a, Fig. 3).

Habitat. At relatively low altitudes; 900-1500 m. In Panama it frequently grows as an epiphyte and occasionally is found in the canopy.


World range: Northeastern and Southeastern U.S.A.; Mexico; Central America; Caribbean, Northern and Southern South America, Brazil; Indo-China, Malesia; Australia, New Zealand.

Sphagnum perichaetiale is surprisingly small for a member of the section Sphagnum. The stem and branch cortical cells generally lack fibrils, and the branch leaf hyaline cells have ringed, elliptic pseudopores grouped in 3's on the outer surface. The green cells of the branch leaves are narrowly and more or less equally exposed on both surfaces.


Plants robust, dark, greasy green above and brown below or yellow-brown throughout, in wide carpets; cortical cells in 3-4 layers, the outermost fibrillosic, with 1-6 irregularly rounded pores; wood cylinder brown. Stem leaves lingulate, broadly
rounded at the apex, with a broad, finely fringed mesh at the margins; hyaline cells often 1-2-divided, on the outer surface almost completely resorbed, on the inner surface with small pores and traces of fibrils, especially near the leaf apex. Branches in fascicles of 4-5 (2 spreading), stoutly club-shaped; cortical cells nested together by funnel-shaped bases porose at the bottom, fibrillose, the inner wall densely cross-fibrillose, the outer surface lacking pores. Branch leaves imbricate, dimorphous: those at the base of branches cucullate-concave, broadly ovate, hyaline-fringed, the hyaline cells on the outer surface strongly convex, almost entirely resorbed toward the leaf tip, with 7-10 large, elliptic commissural pores below, on the inner surface with about 4 small, elliptic corner pores in the upper part of the leaf but more numerous larger, round pores in side regions; leaves of the upper part of branches much larger, denticulate along a marginal resorption furrow, with hyaline cells resorbed on the outer surface only in a few apical cells; green cells in section equilateral-triangular and exposed on the inner surface (or rarely more or less trapezoidal with narrow exposure on the outer surface), the walls of adjacent hyaline cells usually beset with fringe fibrils (sometimes evident only near leaf bases).

Illustrations. Crum (1980, Fig. E); Crum and Anderson (1981, Fig. 5); Crum (1984, Fig. 8).

Habitat. On creek bank; sea level to 100 m.

Distribution in Central America. NICARAGUA. Zelaya: Seymour 4728 (MO).

World range: Northeastern, Southeastern, and South-Central U.S.A.; Mexico; Central America; Caribbean, Northern South America.

The plants, found submerged to emergent in pools and drainage ditches in the eastern United States, apparently grow on wet banks in the tropics. The species is characterized by stout, club-shaped branches with upper leaves denticulate along a marginal resorption furrow and lower leaves much smaller and broadly bordered by a fine-meshed fringe. The branch cortex is made up of funnel-shaped cells nested together. The green cells of branch leaves are broadly triangular, with exposure on the inner surface; the walls of hyaline cells adjacent to the green cells bear fringe fibrils.

2. Sphagnum sect. Rigida
1. Hyaline cells of branch leaves with few to numerous pseudopores (in addition to round pores) on the outer surface; green cells in section elliptic, central, and included; side walls of hyaline cells smooth

5. S. compactum

1. Hyaline cells without pseudopores; green cells triangular, exposed on the outer surface; side walls of hyaline cells usually very finely papillose

6. S. strictum


Plants short, compactly tufted in small, rounded cushions, pale green or brownish, rarely red-brown or pinkish red; cortical cells in 2-3 layers, without fibrils or pores; wood cylinder brown. Stem leaves minute (rarely 1 mm long), concave, shortly lingulate to oblong-triangular, bordered in the lower half, sometimes slightly lacerate at the broad, rounded apex; hyaline cells not divided, without fibrils, on the outer surface without pores or gaps but with membrane pleats, on the inner surface with a membrane gap at the upper end of each cell, small and rounded below but irregular and nearly as large as the cell toward the leaf apex. Branches short, crowded in fascicles of 4-6 (2, rarely 3, spreading); cortical cells in 1 layer, each uniporose at the upper end. Branch leaves imbricate to squarrose, broadly elliptic to oblong-ovate, broadly truncate at an involute-concave or cucullate apex, denticulate along a marginal resorption furrow; hyaline cells slightly convex on both surfaces, on the outer surface with few to numerous round, ringed pores near the commissures, mostly partitioned off by a straight or ring-like fibril and also with few to numerous pseudopores similarly partitioned off, sometimes also with a few irregularly rounded median pores, often with

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5. *Sphagnum compactum*  

membrane pleats, on the inner surface with more or less ringed corner pores, usually in 3's at adjacent angles, and occasional pseudopores at the commissures; green cells, in section, elliptic, central, and entirely included, the adjacent walls of hyaline cells smooth.

**Illustrations.** Crum and Anderson (1981, Fig. 7 A-L); Crum (1984, Fig. 9).

**Habitat.** 3100-3150 m.

**Distribution in Central America.** GUATEMALA. Huehuetenango: Steyermark 49918 (NY).

**World range:** Subarctic America, Western and Eastern Canada, Northwestern, North-Central, Northeastern, Southwestern, and Southeastern U.S.A.; Central America; Northern and Western South America; Northern, Southwestern, Middle, East and Southeastern Europe; Western Asia.

Both *Sphagnum compactum* and *S. strictum* have stem leaves much smaller than branch leaves and branch leaves bordered by a resorption furrow. In both species the cells of the branch cortex are uniformly porose at their upper ends (and more or less retortlike). Essential features of *S. compactum* are its branch leaves with central, fully included green cells and hyaline cells with commissural pseudopores as well as actual pores on the outer surface.


Plants pale brown or yellowish, generally in low, dense, small tufts; cortical cells in 1-3 layers, without pores; wood cylinder yellow-green. Stem leaves very small, bluntly
deltoid, scarcely bordered; hyaline cells not divided, without fibrils or pores, sometimes with membrane pleats in a few apical cells, on the inner surface with an irregular membrane gap in each cell near the leaf apex occupying nearly the entire cell.

Branches usually in fascicles of 5 (2 spreading); cortical cells in 1 layer, each ending in a pore. Branch leaves squarrose-spreading, ovate, involute-concave above and ending in a broad, truncate apex, more or less denticulate along a resorption furrow toward the apex; hyaline cells convex on the inner surface, on the outer surface toward the leaf apex with 2-6 large, round or round-elliptic, non-ringed pores at the commissures, becoming more numerous and more or less ringed below, on the inner surface with 2-4 elliptic, ringed pores especially in corners and often in 2's or 3's at adjacent corners; green cells in section narrowly triangular, often enclosed on the inner surface.

Illustrations. Crum (1980, Fig. F); Crum and Anderson (1981, Fig. 7 M-S); Crum (1984, Fig. 10).

Habitat. 800-1500 m.


World range: Eastern Canada, Northeastern and Southeastern U.S.A.; Mexico; Central America; Caribbean, Northern and Western South America; Northern, Southwestern, Middle, East and Southeastern Europe.

Sphagnum strictum resembles S. compactum but has branch leaf hyaline cells with only pores (pseudopores lacking) on the outer surface and triangular green cells that are exposed on the outer surface. The hyaline cell walls adjacent to the green cells are very finely papillose. The subsp. pappeanum (C. Mull.) Eddy, apparently no more than a robust expression, occurs in tropical Africa and southeastern Asia, as well as tropical America.

3. Sphagnum sect. Isocladus

Plants robust, normally submerged, deep green to red-brown or blackish when wet, shiny and pale green, silvery white, or brownish when dry; cortical cells in 2 layers, those of the epidermis without pores; wood cylinder very hard, yellow-green to brownish. Stem leaves small (about 1 mm long), more or less concave, broadly triangular, rounded at the apex, very indistinctly bordered; hyaline cells rhomboidal, not or rarely divided, without fibrils, on the outer surface with 1 central (sometimes 2-5) large, round to oblong pores usually in a row. Branches short, wide-spreading to somewhat deflexed, not much differentiated as to spreading or pendent types; cortical cells in 1-3 layers, more or less uniform (occasional cells porose but not at all retortlike). Branch leaves crowded, bristly spreading, firm and tubulose when dry, long-elliptic or ligulate to narrowly ovate-oblong, rounded at the narrow tip, with inrolled margins bordered by 2-3 rows of linear cells; hyaline cells nearly plane on both surfaces, very long (15-30:1), linear-sinuose, thick-walled, without fibrils, on the outer surface with (3-)8-14(-21) large, rounded-oblong, non-ringed pores in a single median row, on the inner surface without pores; green cells very broadly exposed on both surfaces.

Illustrations. Crum and Anderson (1981, Fig. 9 A-F); Crum (1984, Fig. 14).
Habitat. Submerged or floating, often in places of fluctuating water level and thus periodically stranded; 150 m.
Distribution in Central America. HONDURAS. Gracia a Dios: Proctor 38851 (MICH, NY, TEFH).
World range: Eastern Canada, Northeastern and Southeastern U.S.A; Central America.

Sphagnum macrophyllum is recognized by its aquatic habitat and bristly groups of short branches scarcely differentiated as to spreading and pendent types. The hyaline cells of the branch leaves are very long with many pores on the outer surface, none on the inner. The single Central American collection represents the var. macrophyllum, characterized by pores on branch leaves only moderately numerous, relatively large,
round, and arranged in a single median row. Along the Atlantic Seaboard of North America, the var. floridanum Aust. is common. It has very many (as many as 64) small, often slitlike pores in two rows on the outer surface of the branch leaf hyaline cells.

4. Sphagnum sect. Cuspidata

1. Branch leaves serrulate in the upper 1/3-1/2; hyaline cells of stem leaves commonly divided (plants aquatic)  
   12. S. trinitense

1. Branch leaves entire (except across the narrow apex); hyaline cells of stem leaves not divided or divided only near the leaf base

2. Stem leaves much like branch leaves in structure, fibrillose throughout, on the outer surface with apical window pores and a few small, somewhat ringed
commissural pores, on the inner surface with numerous round, thin-margined
commissural pores

2. Stem and branch leaves differentiated, with fibrils none or only in the upper cells,
without window pores on the outer surface or commissural pores on the inner

3. Stem cortex in 2-3 layers; stem leaves oblong-ovate; branches in fascicles of 4
9. S. lankesteri

3. Stem cortex in 1 layer; stem leaves narrowly triangular-ovate; branches in fascicles
of 3
10. S. poasense

4. Branch leaves flattened, recurved at the tips, and wavy-margined when dry;
hyaline cells near the apex of stem leaves, on the inner surface, with a large
membrane gap edged by fibril stumps
11. S. sancto-josephense

4. Branch leaves not flattened, recurved at the tips, or notably wavy-margined when dry;
hyaline cells of the upper part of stem leaves, on the inner surface, with
membrane gap none, small, or large but not conspicuously edged by fibril
stumps, if at all
8. S. cuspidatum


Plants normally submerged, slender, flaccid, especially when wet, bright green to
yellow; wood cylinder yellow-green; cortical cells more or less distinctly differentiated
in 2 layers, long, more or less thick-walled, not inflated, without pores. Stem leaves
concave, ovate to ovate-deltoid, blunt or acute, broadly bordered below; hyaline cells
not divided, with or without fibrils above, on the outer surface with small end pores, on
the inner surface largely resorbed near the leaf apex, the gaps decreasing in size below
and at the leaf sides. Branches normally in fascicles of 4 (2 spreading), slenderly
tapered; cortical cells with retort cells differentiated. Branch leaves slightly wavy when dry, long-lanceolate, involute-concave, bordered by 2-4 rows of linear cells; hyaline cells slightly convex on the inner surface, on both surfaces with few, small, inconspicuous end and corner pores; green cells in section broadly trapezoidal, more broadly exposed on the outer surface.

Illustrations. Crum (1980, Fig. K 1-6); Crum and Anderson (1981, Fig. 10 H-S); Crum (1984, Fig. 16).

Habitat. 2500-2600 m.

Distribution in Central America. COSTA RICA. Alajuela: Wilbur 8700 (DUKE); Cartago: Bumby 40-1 (CR); San Jose: Crosby 2579B (DUKE). PANAMA. Bocas del Toro: Davidse et al. 25422 (MO).

World range: Eastern and Western Canada, North-Central, Northeastern, and Southeastern U.S.A.; Central America; Western South America; Northern, Southwestern and Middle Europe; Eastern Asia; Indo-China, Malesia.

Sphagnum cuspidatum grows in shallow water, often in mere puddles subject to drying. The plants are very soft and weak when wet. The branches are noticeably tapered, especially when the plants are drawn from the water. The leaves are somewhat wavy-margined when dry. The branch leaves have hyaline cells with pores few, small, and easily overlooked.


Slender plants in soft, pale yellowish tufts; cortical cells differentiated in 2-3 layers. Stem leaves 1.8-2 mm long, oblong or oblong-ovate, concave-acute, narrowly bordered throughout; hyaline cells fibrillose throughout, not divided, on the outer surface with unringed apical window pores and a few small, somewhat ringed pores scattered along the commissures, on the inner surface with round, thin-margined pores along the commissures (5-11 in the upper median region); green cells broadly exposed on both surfaces but more so on the outer. Branches in fascicles of 4 (2 spreading), noticeably tapered, the young pendent branches in the capitulum not seeming paired; cortical retort
cells differentiated. Branch leaves somewhat flattened and wavy-margined with spreading to recurved tips when dry, 2-2.2 mm long, oblong-lanceolate, long-acuminate, entire, bordered by 2-3 rows of linear cells; hyaline cells bulging on the inner surface, plane or slightly convex on the outer, with somewhat enlarged, round, thin-margined, apical window pores and a few small, rounded-elliptic, more or less ringed pores at corners or along commissures, on the inner surface with numerous round, thin-margined pores along the commissures (8-13 in the upper median region); green cells as seen in section triangular to slightly trapezoidal, broadly exposed on the outer surface, reaching the inner surface and sometimes narrowly exposed.

Illustrations. Crum (1984a, Figs. 1-8).
Habitat. Unknown.
Distribution in Central America. COSTA RICA. Cartago(?): Lankester 1801a (F).
World range: Central America.

The slenderly tapered branches and the similarity of unusually narrow, long-pointed stem and branch leaves characterize the species.

9. Sphagnum lankesteri
10. Sphagnum poasense


Plants slender, in loose, soft, pale yellowish mats; cortical cells well defined in 1
layer; wood cylinder yellowish. Stem leaves 1.5-1.9 mm long, narrowly triangular-ovate, concave-acute, bordered all around by 3-4 rows of linear cells; hyaline cells undivided except near leaf base, fibrillose on both surfaces throughout, on the outer surface with apical window pores and often 1-2(-3) small, ringed pseudopores at side corners, on the inner surface with 5-9 or more rather small, round, thin-margined commissural pores. Branches in fascicles of 3, slenderly tapered, especially when dry; cortical retort cells differentiated. Branch leaves more or less wavy-margined when dry, 1.6-1.8 mm long, narrowly lance-acuminate, tubulose above, entire, bordered by 1-2 rows of linear cells; hyaline cells fibrillose, bulging on the inner surface, on the outer surface with window pores at upper ends and often 1 (sometimes 2) small, round, ringed pseudopores at side corners, on the inner surface with 5-8 rather small, round, thin-margined pores at corners and along commissures; green cells in section triangular to trapezoidal, with exclusive or broader exposure on the outer surface.

Habitat. On peaty soil; 2600 m.
Distribution in Central America. COSTA RICA. Alajuela: Richards 6036 (MICH).
World range: Central America.

The plants resemble small expressions of Sphagnum cuspidatum Hoffm., but the stem leaves are fibrillose throughout and have pores similar to those of branch leaves. On their outer surfaces, the hyaline cells have small window pores at their upper ends, and the inner surface shows numerous round, thin-margined commissural pores. The branches are noticeably tapered, especially when dry.


Plants rather slender, in soft, loose, yellow-green tufts. Young pendent branches (in the capitulum) often seeming paired; cortex of large thin-walled cells in 2 layers, without epidermal pores; wood cylinder yellowish. Stem leaves ca. 1.4 mm long, somewhat concave, oblong-ovate, acute, not noticeably erose at the tip or bordered,
hyaline cells undivided, on the outer surface with fibrils and occasional end pores near the leaf tip, on the inner surface largely resorbed, near the apex with stumps of fibrils surrounding large membrane gaps. Branches in fascicles of 4-5 (2-3 spreading);

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11. Sphagnum sancto-josephense          12. Sphagnum trinitense

cortical retort cells differentiated. Branch leaves flattened out and wavy-margined when dry, concave and 5-ranked when moist, 1.7-1.8 mm long, oblong-ovate, bordered by several rows of linear cells; hyaline cells somewhat convex on the inner surface, on the outer with 2-4 small, somewhat ringed, round or elliptic end and corner pores, on the inner surface with 4-11 large, round, thin-margined pores arranged more or less along the commissures; green cells, as seen in section, triangular, exposed on the outer surface, not reaching the inner.

Illustrations. Crum and Crosby (1974, Figs. 1-14); Crum (1980, Fig. J).
Habitat. At moderate to high elevations of 2000-3300 m.
Distribution in Central America. COSTA RICA. Alajuela: Gomez 22827 (MICH, MO); Cartago: Wilbur 20433 (DUKE); San Jose: Gomez 2114 (MO).
World range: Central America; Northern and Western South America.

This species has branch leaves flattened out and wavy-margined when dry. The hyaline cells of the branch leaves have few small end and corner pores on the outer surface and numerous large, round pores on the inner. The hyaline cells of the stem leaves, near the apex on the inner surface, have large gaps (nearly as large as the cells) surrounded by fibril stumps.

Sphagnum recurvum P. Beauv. (S. pulchricoma C. Mull.) can be expected in Central America, as it is known from Cuba, Mexico, and northern South America in addition to a wide range in North America, Asia, and Europe. It resembles S. sancto-josephense, but its stem leaves are broadly rounded-truncate and erose-fringed at the apex, and the upper hyaline cells, on the inner surface, although largely resorbed, have gaps that are not edged by fibril stumps.

   cuspidatum var. serrulatum (Schlieph.) Schlieph., Irmischia 2: 67. 1882.

Plants relatively robust (to 12, rarely 45 cm long), pale yellow-green to yellowish, in lax, floating mats; cortical cells long, narrow, poorly differentiated in 1-3 layers; wood cylinder yellowish. Stem leaves concave, oblong to ovate, acute to blunt or rounded-obtuse, often erose at the apex, not or somewhat broad-bordered at base; hyaline cells fibrillos throughout or sometimes only above, few to many (usually) 1-divided, on the outer surface without pores or gaps, on the inner surface with fibrils and 2-5 small, round pores or with fibrils vestigial to lacking and 2-4 median gaps, or the membrane largely resorbed, both surfaces largely resorbed near the leaf apex. Branches in fascicles of 4 (rarely 5) (with 2 deflexed), sometimes cuspidate-tipped but more often ending in a loose tuft of long-tapered leaves that are flexuous-contorted when dry; retort cells differentiated. Branch leaves when young (in the capitulum) often rather short and broadly truncate or rounded at the apex, the others narrowly lanceolate and long-tapered (longer and narrower toward the branch tips), involute-concave when moist, flatter and wavy-margined when dry, with bordered margins serrulate in the upper third, half, or nearly throughout (more distinctly so at tips of long upper leaves),
hyaline cells slightly convex on the inner surface; on the outer surface with pores 1-2 (rarely 3) very small, inconspicuous, and round, at ends and corners, sometimes lacking, on the inner surface with 3-6 (rarely 8) small, indistinct, unringed, round pores at ends and corners, sometimes also at commissures.

Illustrations. Crum (1980, Fig K 7-8); Crum and Anderson (1981, Fig. 10 T-W); Crum (1984, Fig. 17 A-B, as S. cuspidatum var. serrulatum).

Habitat. Near sea level.


World range: Eastern Canada, Northeastern and Southeastern North America; Central America; Caribbean, Northern South America, Brazil; Middle Europe.

More robust than Sphagnum cuspidatum, this species is especially characterized by distinct toothing at the leaf margins (most noticeably in the long leaves at the ends of branches) and by leaf tips loosely flexuous-contorted when dry. The hyaline cells of the stem leaves tend to be divided.

5. Sphagnum sect. Subsecunda

1. Branches slenderly tapered; stem leaves fibrillose throughout; hyaline cells of both stem and branch leaves with pores (and pseudopores) few, not conspicuously in commissural rows
   15. S. trirameum

1. Branches not conspicuously tapered; stem leaves fibrillose in the upper 1/3-1/2 or more

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2. Branches in fascicles of 4, 2 pendent; hyaline cells of both stem and branch leaves with pores crowded in commissural rows
   14. S. subsecundum var. rufescens

2. Branches in fascicles of 1-3, pendent branches scarcely differentiated; hyaline cells of stem and branch leaves with pores few or numerous and in interrupted commissural rows
   13. S. platyphyllum


Plants stout, in loose, limp, yellowish to green patches; capitulum not much differentiated but the terminal bud large (especially noticeable when wet); cortical cells in 2-3 layers, mostly porose at the upper ends; wood cylinder dark brown. Stem leaves spreading, concave, broadly oblong-elliptic and rounded-obtuse, 1.5-2(3) mm long, much like branch leaves in size, shape, and structure; hyaline cells fibrillose nearly throughout, rarely divided, on the outer surface with few to many small pores, restricted to ends and corners or in interrupted commissural rows, on the inner surface with pores few, small, at ends and corners. Branches straight, tumid, 1-3 per fascicle, not differentiated into spreading and pendent types and not concealing the stem. Branch

13. Sphagnum platyphyllum 14. Sphagnum subsecundum var. rufescens

leaves erect and imbricate, deeply concave, 1.6-2.5 mm long, broadly oblong-ovate; hyaline cells on the outer surface with few to numerous small, scattered pores or sometimes many in commissural rows; on the inner surface with pores small, few or
Illustrations. Andrus (1980, Fig. 16); Crum (1984, Fig. 38 A-B as S. subsecundum var. platyphyllum).

Habitat. In standing water; 2800-3000 m.

Distribution in Central America. COSTA RICA. Cartago: Karlin (BING, MICH, NY).

World range: Subarctic America, Western and Eastern Canada, Northwestern, North-Central, Northeastern, and Southwestern U.S.A.; Central America; Northern Europe; Siberia, Eastern Asia.

The plants have tumid branches, one to three per fascicle and scarcely differentiated as to spreading and pendent types. The terminal bud is prominent. The stem leaves are fibrillose nearly throughout.


Plants of medium size, green or, more commonly, yellow-brown to orange; stems brown; cortical cells in 1 layer, without pores; wood cylinder yellow-green to brown. Stem leaves 1.3-2.5 mm long, oblong-ovate to lingulate, rounded at the apex, the border not much expanded at base; hyaline cells commonly divided and often with membrane pleats, fibrillose in the upper 1/3-1/2 or nearly throughout, with many elliptic commissural pores on the outer surface, few to numerous on the inner. Branches often curved, in fascicles of 4 (2 spreading); cortical retort cells differentiated. Branch leaves appressed or more or less secund, 1.5-2.5 mm long, rather narrowly to broadly oblong-ovate; pores more or less contiguous and commissural on the outer surface, few or none on the inner; green cells in section more or less truncately elliptic, exposed equally or somewhat more broadly on the outer surface.
Illustrations. Crum (1980, Fig. M 3-4); Crum and Anderson (1981, Fig. 16 H); Crum (1984, Fig. 34 D-E).


16. Sphagnum gomezii


World range: Subarctic America, Western and Eastern Canada, Northwestern, North-Central, Northeastern, Southwestern, South-Central, and Southeastern U.S.A.; Mexico; Central America; Western South America; Northern, Southwestern, Middle, East and Southeastern Europe; Eastern Asia; Australia and New Zealand.

Sphagnum subsecundum most commonly has young branches of the capitulum, and sometimes older branches as well, curved and leaves upcurved-secund. The hyaline cells of the branch leaves have many crowded commissural pores. The var. rufescens sometimes has relatively narrow, secund branch leaves and at other times broad, erect-appressed leaves. The stem cortex is one-layered, and the stem leaves are oblong-lingulate and fibrillose in the upper half or nearly throughout.

Plants small, in soft, loose, yellow-green mats; cortical cells 1-layered, without pores; wood cylinder yellow. Stem leaves 1.4 mm long, oblong-triangular, bluntly obtuse, somewhat concave at the tip, bordered to the base by 3-4 rows of linear cells, entire; hyaline cells fibrillose on both surfaces throughout, often 1-divided, on the outer surface with membrane pleats and 1-6 small commissural and end pores and pseudopores, often in short rows of 2 or 3, on the inner surface with very few small end pores. Branches in fascicles of 3, all spreading, slenderly tapered; cortical retort cells differentiated. Branch leaves loosely spreading, 1.2-1.4 mm long, concave, ovate, bordered by 4-5 rows of linear cells, entire except at the narrow, truncate apex; hyaline cells moderately convex on both surfaces, on the outer surface with membrane pleats and few small end and commissural pores and pseudopores and often cross-connecting fibrils, on the inner surface with very few small pores at ends and corners; green cells in section very narrowly rectangular, equally exposed on both surfaces.

Illustrations. Crum (1989, Figs. 31-37).
Habitat. On wet, calcareous rocks and on soil; 90-1020 m.
Distribution in Central America. BELIZE. Cayo: Davidse & Brant 33111 (MO).
GUATEMALA. Baja Verapaz: Sharp 5143 (MICH, MO, TENN).
World range: Central America.

Special features of this species are slenderly tapered branches, stem leaves fibrillose throughout, and stem and branch leaf hyalocysts with membrane pleats and very few pores. The hyaline cells of the stem leaf cells, especially, have a scattering of pseudopores in short commissural rows, demonstrating a relationship to sect. Subsecunda. Sphagnum richardsianum Crum, of Mexico, is similar in aspect, but has a 2-layered stem cortex, larger stem and branch leaves (1.5-2.2 mm long) that are broader, flatter, and broader-tipped, and the green cells of its branch leaves are broader and more broadly exposed. Its branches are not noticeably tapered.
6. Sphagnum sect. Acutifolia

1. Epidermal cells of stems with pores none or rare; hyaline cells of stem leaves much divided and perforated by round to oblong membrane gaps
   16. S. gomezii

1. Epidermal cells of stems commonly porose; hyaline cells of stem leaves not or 1-2-divided, with gaps few or none

2. Branch leaf hyaline cells at apex with a few scattered, tiny, round pores on the outer surface, and in lower cells with ringed, elliptic pores and pseudopores few or none; green cells of branch leaves narrowly exposed on both surfaces
   18. S. meridense

2. Branch leaf hyaline cells at the apex with elliptic, ringed pores on the outer surface throughout; green cells of branch leaves more or less triangular in section, with exclusive or broader exposure on the inner surface

3. Branch leaf hyaline cells at the leaf tip, on the outer surface, with small, ringed, elliptic pores conspicuously grouped in 3's at adjacent angles; hyaline cells of stem leaves with more or less rudimentary fibrils and membrane pleats on the outer surface, largely resorbed on the inner
   19. S. sparsum

3. Branch leaf hyaline cells with large, ringed, elliptic commissural pores throughout; hyaline cells of stem leaves fibrillose in the upper half or more, on the outer surface with many ringed, elliptic commissural pores, on the inner with rather numerous round, porelike gaps, especially at corners
   17. S. limbatum

   S. subdivisum Crum, Bryologist 92: 98. 1989, syn. nov.

   Plants slender, pale, pinkish or pinkish violet, especially in the capitulum; stems and branches red; cortical cells in 3 layers, rectangular, rarely uniporose; wood cylinder red. Stem leaves 1.6-2 mm long, oblong-ovate, broadly acute, concave toward the apex, sometimes more or less pinched at the tip, bordered all around but not wide-bordered at base; hyaline cells divided into 2-4 compartments, on the outer surface
more or less fibrillose toward the leaf tip, with 1-4 large, round or oval membrane
gaps or occasionally membrane pleats, on the inner surface largely resorbed or some
cells with 1 or more large, round or oval gaps and some few vestiges of fibrils and
some cells with pleats but no fibrils. Branches in fascicles of 3 (2 spreading); cortical
retort cells differentiated. Branch leaves 1.4-1.6 mm long, oblong-lanceolate, bordered
by 2-3 rows of linear cells; hyaline cells strongly bulging on the outer surface, nearly
plane on the inner, on the outer surface with numerous ringed, narrowly elliptic
commissural pores, those at adjacent cell corners noticeably in 3's, on the inner surface
with pores lacking or with 1(-2) large, round, unringed pores, at side regions with 1-3

round gaps about as wide as the cells, at the basal margins with as many as 5 gaps;
green cells in section triangular to trapezoidal, with exclusive or broader exposure on
the inner surface.

Illustrations. Crum (1984a, Figs. 9-16); Crum (1989, Figs. 9-16, as S. subdivisum).

Habitat. At high elevations; 2000-2100 m.
Distribution in Central America. COSTA RICA. Cartago/San Jose: Murray &
Johnson 805 (MICH); San Jose: Gomez 2124 (F).
World range: Central America.

Much-divided hyaline cells of the stem leaves and considerable resorption on both
surfaces define this species. The roundish gaps on the outer surfaces are noticeable.
The near absence of pores in the stem cortex distinguishes this from other members of
the section Acutifolia likely to be seen in Central America. Forms of Sphagnum
sparsum that have stem leaves with hyaline cells perforated by gaps can be recognized
by small pores on the outer surface of the branch leaf hyalocysts and porose epidermal
Cells of the stems.

   (Besch.) Warnst. in Engler, Pflanzenr. 51: 112. 1911.
   S. lesueurii Warnst., Hedwigia 29: 205. 1890, nom. illeg. incl. sp. prior, S. antillarum
   Besch.

   Plants of moderate size, sometimes relatively robust, pale green, pinkish above;
   cortical cells in 2-3 layers, those of the outer layer mostly porose at the upper ends;
   wood cylinder yellow-green. Stem leaves relatively large, narrowly oblong-triangular to
   lingulate, concave-acute, narrowly bordered throughout; hyaline cells divided 1-several
   times in the lower half of the leaf, fibrillose in the upper half or more, on the outer
   surface with many ringed, elliptic commissural pores, passing into large gaps below, on
   the inner surface with numerous large, thin-margined, porelike gaps, 4-5 above, more
   below. Branches in fascicles of 4 (2 spreading); cortical retort cells differentiated.
   Branch leaves broad and loosely spreading when dry, more concave, narrower, and
   erect when moist, ovate, more or less abruptly pointed, narrowly bordered by linear
   cells; hyaline cells on the outer surface very convex, with many ringed, elliptic
   commissural pores on the outer surface, on the inner surface with 2, rarely as many as
   6, round, non-ringed pores (especially in side corners), more numerous toward leaf
   margins; green cells in section exclusively or more broadly exposed on the inner
   surface (but in surface view, owing to convexity of hyaline cells, appearing equally
   exposed on both surfaces).

   Illustrations. Warnstorf (1890, Pl. 5, Figs. 14 a-b, Pl. 6, Fig. 7); Warnstorf (1911,
   Fig. 25 B).

   Habitat. At moderate to fairly high elevations of 2000-3300 m.
   Distribution in Central America. GUATEMALA. Baja Verapaz: Sharp 2770 (MO);
   Huehuetenango: Steyermark 51950 (NY). COSTA RICA. Alajuela: Gomez et al. 23985
   (MICH, MO); Cartago: Crosby & Crosby 6181 (MO); Puntarenas: Almeda 6798 (MO);
   San Jose: Crosby 10944 (MO);
World range: Mexico; Central America; Caribbean, Western South America.

When well developed, Sphagnum limbatum has much the same appearance as S. meridense, but its branch leaves have, on the outer surface, numerous large, ringed commissural pores (and no tiny, round pores near the leaf tips) and, on the inner surface, only a few non-ringed pores. The green cells, in section, are exclusively or

17. Sphagnum limbatum

18. Sphagnum meridense

more broadly exposed on the inner surface, but this is difficult to demonstrate in surface views owing to the considerable convexity of the hyaline cells. The stem leaves have numerous ringed, elliptic commissural pores on the outer surfaces of the hyaline cells and round commissural pores or gaps on the inner surface. Confusion with S. tenerum Sull. & Lesq. is possible, but the porosity of the epidermal cells of the stem make S. limbatum certain of identification. Sphagnum tenerum, common in coastal plains of eastern North America and also found in a few scattered South American localities, can perhaps be expected in Central America.

Plants tall, loosely tufted in soft, deep mounds, pale green to bright pink; cortical cells in 2-3 layers, the outer layer with pores at the upper ends of many or few cells; wood cylinder yellowish to pinkish. Stem leaves 1.5-2 mm long, oblong-ovate, broadly concave-acute; border rather strong above, not or slightly broadened at base; hyaline cells not or rarely 1-divided above, sometimes divided toward the leaf base, usually without fibrils or pores but exceedingly variable, on the outer surface often with membrane pleats but no pores or gaps, sometimes more or less fibrillose near the apex, on the inner surface without pores or gaps or sometimes with 1-5 irregularly round or rounded-elliptic, unringed commissural pores. Branches in fascicles of 5-6 (2-3 spreading); cortical retort cells differentiated. Branch leaves rather widely spaced and loosely erect-spreading, deeply but broadly concave, 1.3-2 mm long, broadly oblong-ovate or elliptic, gradually narrowed to a short, involute-concave point (more concave, narrower, and more abruptly short-pointed when moist), bordered by 1-3 rows of linear cells; hyaline cells slightly convex on the inner surface, somewhat more so on the outer, on the outer surface often with membrane pleats and near the leaf apex usually with few to numerous (3-8) very small, round or elliptic, ringed pores in ends or corners, sometimes also on cell middles, and usually a few larger but inconspicuous, elliptic corner pores in median and lower portions of the leaf, on the inner surface with 3-8 large, round, distinct but unringed pores at ends and corners and along the commissures; green cells in section lenticular, equally exposed on both surfaces because of thickened cell ends.

Illustrations. Crum (1980, Fig. P); Crum (1984, Fig. 44).
Habitat. At moderate to fairly high altitudes; 700-3000 m.
Distribution in Central America. GUATEMALA. Alta Verapaz: Standley 92577 (NY); Chiquimula: Steyermark 30989 (NY); El Progreso: Sharp 2801 (NY, MO); Huehuetenango: Sharp 4883 (MO); Zacapa: Steyermark 43257 (NY). EL SALVADOR.
Santa Ana: Watson ES-0038 (MO). HONDURAS. Comayagua: Allen 11006 (MICH, MO, TEFH); Cortes: Allen 14058 (MICH, MO, TEFH); Lempira: Allen 11223 (MICH, MO, TEFH); Morazan: Olson 84-48 (MO); Olancho: Allen 12751 (MICH, MO, TEFH). COSTA RICA. Alajuela: Stark 3358 (MO); Cartago: Crosby & Crosby 6181 (MO); Heredia: Dodge 6075 (NY, DUKE); Limon: Davidse et al. 28654 (MO); Puntarenas: Herrera 3520 (MICH, MO); San Jose: Crosby 10889 (MO). PANAMA. Chiriqui: Antonio 2629 (MO).

World range: Mexico; Central America; Caribbean, Western and Northern South America.

This beautiful moss, tall and stately, may be a pale green, but it is more often some shade of pink. Its branch leaves are rather widely spaced, erect-spreading, broadly concave, and abruptly narrowed to a short, involute point. The branch leaf hyaline cells generally have few pores on the outer surface, except near the leaf tip where they are small and elliptic and nearly always mingled with tiny, round, ringed pores, some of them scattered over cell middles. On the inner surface, the pores are rather large and numerous, round, and thin-marginated. The branch leaf green cells are narrowly and equally exposed on both surfaces. The stem leaves are remarkably variable. Pores, gaps, and fibrils are generally lacking, but on the inner surface there are sometimes gaps or few to numerous large, round to elliptic, unringed commissural pores. The stem epidermis has some to many porose cells.

S. apollinairei Par. & Warnst. ex Warnst., Hedwigia 47: 114. 1907.

Plants slender, in compact, pink or pink-tinged cushions; cortical cells in 3-4 layers, those of the epidermis mostly porose at the upper ends; wood cylinder pale, yellow to pinkish. Stem leaves 1.4-1.6 mm long, oblong-lanceolate to triangular-ovate, concave-pointed; border not much broadened at base; hyaline cells usually short, mostly 1(-2)-divided, on the outer surface with membrane pleats, more or less rudimentary fibrils and sometimes a few scattered, round membrane gaps in the upper half or less (sometimes with long, narrow, fibrillose cells with numerous round to oblong membrane gaps), on the inner surface mostly resorbed. Branches in fascicles of 4 (2 spreading); cortical retort cells differentiated. Branch leaves erect when moist, slightly spreading at the tips when dry, not ranked, 1.1-1.5 mm long, broadly oblong-lanceolate, concave-acuminate, bordered by 2-3 rows of linear cells; hyaline cells decidedly convex, on the outer surface near the leaf apex with 3-8 small, elliptic,
ringed commissural pores (noticeably grouped in 3's at adjacent cell angles), larger below, on the inner surface without pores in the upper median region or with a few small, round, ringed pseudopores and rarely a few large, round, unringed pores at ends and corners, toward the leaf margins with numerous large, round, thin-marginated pores; green cells broadly triangular to trapezoidal, exposed exclusively or more broadly on the inner surface.

Illustrations. Crum (1980, Fig. 0).

Habitat. At relatively high elevations of 2480-3700 m.


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19. Sphagnum sparsum                1. Andreaea alpestris

(MO); Puntarenas: Gomez 22681 (MICH, MO); San Jose: Crosby & Crosby 5724 (MICH, MO). PANAMA. Veraguas: Hammel & Kress 8579 (DUKE).

World range: Mexico; Central America; Western South America, Brazil.
Sphagnum sparsum resembles the wide-ranging S. capillifolium (Ehrh.) Hedw. of the North, but the stem epidermal cells are porose, and the stem leaves have hyaline cells once- or twice-divided with membrane pleats on the outer surface and a poor development of fibrils. The branch leaves have small, ringed, elliptic commissural pores on the outer surface near the apex.

Normally the stem leaf hyaline cells are short and have membrane pleats, but they are sometimes more elongate with well-formed fibrils and numerous round to oblong membrane gaps. This expression, described as S. apollinairei, occurs sporadically throughout the range of the species.

**ANDREAEACEAE**

Plants small to medium sized, caespitose, dark brown, reddish, or blackish, rigid and brittle when dry; stems erect, irregularly branched, central strands absent. Leaves lanceolate, ovate or obovate, broadly acute to obtuse, not bordered; costate or ecostate; cells short above, elongate at base, incrassate throughout, variably porose and sinuose, papillose or smooth; alar cells not or weakly differentiated. Cladoautoicous. Sporophytes terminal, elevated on a pseudopodium. Setae absent; capsules shortly exserted, elliptic, dehiscent by 4-8 longitudinal slits. Peristome absent. Calyptrae small, campanulate-mitrata. Spores brown, smooth.

The family consists of a single genus.


A genus of worldwide distribution, but restricted to granitic rocks at relatively high altitudes or latitudes. In Central America this is a genus of small plants occurring in reddish brown to black, brittle mats. The genus is remarkably diverse in the Andean region of South America. There are three species in Central America.

1. Leaves costate
3. A. subulata

1. Leaves ecostate

2. Leaves imbricate-appressed when dry, without a whitish bloom; leaf apices obtuse; upper leaf cells not or weakly porose; dorsal papillae absent or weakly developed

1. A. alpestris

2. Leaves spreading to appressed when dry, frequently with a whitish bloom; leaf apices acute; upper leaf cells strongly porose; dorsal papillae well-developed

2. A. rupestris


Plants small, 1-2 cm high. Leaves without a whitish bloom, imbricate-appressed, lanceolate, concave, weakly cucullate above, somewhat constricted above the base, weakly panduriform, 0.5-1.0 mm long, apices straight, obtuse; margins erect somewhat incurved above; lamina unistratose or bistratose in streaks; ecostate; upper leaf cells irregularly short rectangular to quadrate or oval, 7-10 um | 5 um, firm-walled to incrassate, not pitted; lower leaf cells 12-30 um | 7 um, yellowish, long-rectangular, incrassate, pitted and sinuous; cells smooth or with low, weak dorsal papillae. Perichaetial leaves differentiated, sheathing, convolute. Sporophytes as in the genus. Spores not seen.

Illustrations. Sharp (1936, Pl. 1 C); Bartram (1949, Fig. 3 D, as var. rupestris); Nyholm (1969, Fig. 453 a-aaa); Smith (1978, Fig. 30 8-9); Murray (1987, Fig. 9); Murray (1988, Fig. 24).

Habitat. Granitic rocks; 3000-4400 m.

Distribution in Central America. GUATEMALA. Quezaltenango: Steyermark 34209
(F, FH); Totonicapan: Sharp 2640 (FH); San Marcos: Steyermark 35786 (F, FH).
HONDURAS. Lempira: Allen 11510 (MO, TEFH). COSTA RICA. San Jose: Karlin 9006-0651 (MO).

World range: Subarctic America, Eastern and Western Canada, Northwestern U.S.A.; Central America; Northern, Middle, and East Europe; Siberia, Soviet Far East.

This species is separated from Andreaea rupestris by its smaller size, imbricate, obtuse leaves, the lack or weak expression of dorsal papillae, and its smaller, non-porose upper leaf cells. The taxon has been treated as a variety, subspecies or synonym of A. rupestris, but most recently Murray (1987) maintained it at the specific rank. In Central America A. alpestris appears distinctive, but it cannot be critically evaluated because it is known from only a few collections. Murray (1987) considered the Central American collections of A. alpestris misnamed but offered no opinion on their identity. The Central American species appear to agree in all particulars with her 1987 treatment of Andreaea alpestris.


Plants small to medium sized, 1-3 cm high. Leaves frequently with a whitish bloom, 1-2 mm long, crowded, spreading to appressed when dry, ovate- to oblong-lanceolate, weakly constricted and panduriform above the base, concave; apices acute to bluntly acute; margins thick, entire (perichaetial leaves shortly and bluntly dentate); ecostate; upper median cells 15-19 um | 10 um, short-rectangular, upper marginal cells quadrate, median cells distinctly longer than the marginal cells, strongly incrassate, and porose throughout, the upper cells with stellate lumina commonly with large, thick papillae on the dorsal surface (occasionally on ventral), basal cells 50-75 um | 10 um, long rectangular. Sporophytes not seen in Central America.

Illustrations. Hedwig (1801, Tab. 7 G-N); Husnot (1884, Pl. 1); Braithwaite (1887, Pl. 1 A); Brotherus (1914, Pl. 1, as A. petrophila); Grout (1903, Pl. 6, as A. petrophila); Dixon and Jameson (1924, Tab. 4 A, as A. petrophila); Bartram (1933, Fig. 3); Sharp (1936, Pl. 1 A); Bartram (1949, Fig. 3 A-C); Nyholm (1969, Fig. 453 A); Allison and Child (1971, p. 33); Lawton (1971, Pl. 4 19-29); Scott and Stone (1976, Pl. 1); Magill (1981, Fig. 7 11-24); Smith (1978, Fig. 30 5-7); Crum and Anderson (1981, Fig. 24 A-F); Ireland (1982, Pl. 45); Crum (1983, Fig. 15 A-E); Abramov and Abramova (1983, Pl. 3); Murray (1987, Fig. 7); Murray (1988, Fig. 21).
Habitat. On siliceous rocks; 2900-4600 m.

Distribution in Central America. GUATEMALA. San Marcos: Steyermark 35542 (F, FH); Solola: Steyermark 47494 (F, FH). COSTA RICA. San Jose: Griffin et al. 19983 (US).

World range: Subarctic America, Western and Eastern Canada, Northwestern, North-Central, Northeastern, Southwestern, and Southeastern U.S.A.; Mexico; Central America; Caribbean, Western and Northern South America, Brazil; Northern, Southwestern, Middle, East and Southeastern Europe; Western Asia, Caucasus, Soviet Middle Asia, Siberia, Soviet Far East, Mongolia, China, Eastern Asia; Macaronesia, Southern Africa; Australia, New Zealand; Antarctica.

This variable species is separated from Andreaea alpestris by its narrower, densely papillose leaves, longer, sinuose and porose upper median leaf cells, and acute leaf apices. When dry the leaves are spreading to appressed rather than imbricate-appressed. In general aspect this species resembles a Grimmia or Bryomanginia, two genera with costate leaves.

Andreaea turgescens Schimp. ex C. Mull has been reported from Costa Rica (Bartram 1928), but the specimen on which the report was based (Standley 43610) could not be located in either US or FH. Iwatsuki (in Sharp, Crum and Eckel 1993) treats A. turgescens as a synonym of A. rupestris.
2. Andreaea rupestris

3. Andreaea subulata


Plants small, 1-2 cm high. Leaves blackish red, without a whitish bloom, falcate-secund, long-subulate from an ovate to oblong base, concave, 1-2 mm long, apices acute; margins plane; lamina unistratose; costa 0.33 to 0.5 the width of the leaf base, filling or nearly filling the subula at midleaf; median leaf cells short rectangular to quadrate, 10-12 um, very thick-walled with rounded lumina, not pitted; lower leaf cells rectangular 16-18 um long, very thick-walled, pitted, yellowish. Perichaetial leaves sheathing, convolute. Sporophytes not seen in Central America.

Illustrations. Hooker (1844, Pl. 57, Fig. 1); Scott and Stone (1976, Pl. 2); Magill (1981, Figs. 1-12).

Habitat. On granitic boulders in stream at edge of cataract; 2480 m.

Distribution in Central America. HONDURAS. Lempira: Allen 11493 (MO, TEFH).

World range: Central America; Western and Southern South America, Brazil; East Tropical Africa, Southern Africa, West Indian Ocean; Australia, New Zealand; Subantarctic Islands.

This species closely resembles Blindia in color and aspect as well its occurrence on rocks or boulders in streams, but vegetatively it differs in its lack of alar cell differentiation and its shorter, thicker-walled leaf cells. From members of the Grimmiaeaceae it differs by its short, thick-walled leaf cells.
SELIGERIACEAE

Plants small, gregarious or tufted, erect, simple or sparsely and irregularly branched, not tomentose. Leaves subulate-acuminate from a narrow base; costa single, strong, excurrent or percurrent; cells short above, smooth, alar cells well-developed or not differentiated. Dioicous or autoicous. Setae erect or curved-cygneous; capsules erect, stomata present; annuli large, compound or simple; opercula rostrate, straight or oblique; peristome teeth absent or single, 16, truncate or elongate, entire or split at the tip. Calyptrae mitrate or cucullate.

The genera in this family are gametophytically diverse, but all possess the same distinctive "double" peristome which consists of an "endostome" (with a lightly thickened ventral surface and strongly thickened dorsal trabeculae) and an "exostome" that either adheres to the margins of the teeth as a thin membrane or occurs as a prostome at the base of the teeth (Edwards 1979).

Key to the genera

1. Plants minute; alar cells not differentiated; costa percurrent; annuli compound; calyptrae mitrate; autoicous
   1. Brachydontium

1. Plants medium sized; alar cells well-differentiated, inflated, reddish brown; costa excurrent; annuli simple; calyptrae cucullate; dioicous
   2. Blindia


Plants minute, gregarious. Leaves subulate; costa strong, single; cells smooth, short above, longer at base, alar cells not differentiated. Autoicous. Setae elongate, cygneous or straight; capsules erect, stomata present; annuli large, compound; opercula rostrate, straight; peristome teeth absent or 16, short and truncate, papillose. Calyptrae mitrate.

Brachydontium is a genus of minute, acrocarpous mosses found throughout the world. The genus is predominately autoicous (B. curvisetum Crum is dioicous). It has
strongly costate leaves, smooth, firm-walled leaf cells and undifferentiated alar cells. It is separated from other gametophytically similar mosses (except Campylostelium) by its mitrate calyptra. Also distinctive are its shortly truncate, papillose peristome teeth that barely exceed a large, compound annulus. The setae in most species are cygneous.


Plants yellowish green; stems to 1 mm long, simple or with one or two short branches at base. Leaves 0.8-1.8 mm long, erect-patent at base, flexuous above, ovate to oblong sheathing at base, linear above; apex rounded-obtuse; margins nearly entire, narrowly recurved below; costa ending near the apex; upper cells quadrate to short rectangular, thick-walled with rounded lumens, 5-7 um wide; cells above the sheathing base oblong, thickened at the corners, 16-32 um | 8 um; basal cells firm but thin-walled, 20-58 um | 10-13 um. Autoicous. Setae yellow, 0.9-1.2 mm long, cygneous when moist; capsules brown, cylindric, 0.6-0.85 mm long, slightly swollen at base; opercula yellow, low conic-rostrate, beak slightly oblique, 400 um long; annuli large and compound, consisting of 3-4 rows of cells, the outer row of short thick-walled cells remaining on the operculum, the inner rows larger, thinner-walled detaching from or remaining on the capsule mouth; peristome teeth short, truncate, papillose, 60-75 um long, inserted below the capsule mouth. Calyptrae several-lobed and often ragged at base, yellowish, 700-750 um.

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Brachydontium olsonii  

Habitat. On bark(?).
Distribution in Central America. HONDURAS. Comayagua: Olson 84-66E (MO).
World range: Central America.

This species differs from other Brachydontium species in its shorter setae (0.9-1.2 mm vs. 1.7-3.0 mm), longer (0.6-0.85 mm vs. 0.45-0.7 mm), broader (2.5-3.5:1 vs. 1.3-2:1), and smooth capsules, and leaves with obtuse apices and narrowly recurved margins. The presence of this species on bark is notable. However, the Honduran collection was separated from a mixed collection, which may have been a multiple gathering.

Based on sporophytic features B. olsonii appears close to B. flexisetum (Hampe) Par. (South America-Africa). Brachydontium curvisetum (Mexico) appears to be the same as B. flexisetum, but it is reported to be dioicous rather than autoicous.


Plants medium sized, brown to yellow-green. Leaves lanceolate, erect-spreading to secund; costa single, strong, excurrent; cells smooth, incrassate, upper cells short, basal cells linear, alar cells well-developed, inflated, red-brown. Dioicous. Setae erect; capsules exserted, erect, stomata present; annuli simple; peristome teeth 16, lanceolate, smooth. Calyptrae cucullate.

Plants slender, tufted, greenish yellow to brownish; stems sub-erect, 2-7 cm long, branches irregular, central strand absent. Leaves erect to erect-spreading or secund, evenly spaced, lanceolate, 3.0-3.5 mm long, apex abruptly long-subulate; margins entire below, denticulate to sub-entire above, erect or incurved; costa single, long-excurrent, in transverse section guide cells not differentiated, consisting of only stelar cells; cells smooth and incrassate throughout, upper cells short and irregularly rectangular, basal cells linear, 18-55 µm | 5-9 µm, reddish above; alar cells strongly differentiated, forming distinct groups, dark, abruptly inflated, thin-walled, reddish brown. Sporophytes unknown in Central America [description from Crum and Anderson, 1981] "setae 5-11 mm long, straight or flexuous-curved above; capsules about 1 mm long, obovoid, becoming pyriform and constricted below the mouth when dry and empty; peristome teeth lanceolate, acute, entire or more-or-less split at the tip dark red or red-brown. Spores 13-18 µm, smooth or minutely roughened, brownish."

Illustrations. Bartram (1949, Fig. 14 E-H); Crum and Anderson (1981, Fig. 61 A-H); Ireland (1982, Pl. 68 1-9); Bartlett and Vitt (1986, Figs. 1-9); Noguchi (1987, Fig. 49 B).

Habitat. On wet sand; 2250 m.

Distribution in Central America. GUATEMALA. Quezaltenango: Standley 83684 (F, FH).

World range: Subarctic America, Western and Eastern Canada, Northwestern, North-Central, Northeastern, Southwestern, and Southwestern U.S.A.; Central America; Western South America; Northern, Southwestern, Middle, East and Southeastern Europe; Caucasus, Soviet Middle Asia, Siberia, Soviet Far East, China, Eastern Asia; Indian Subcontinent; Macaronesia, West-Central Tropical Africa, Western Indian Ocean.

Blindia acuta is very close to the Southern Hemispheric B. magellanica. Bartlett and Vitt (1986) distinguished the two by the smaller overall size (particularly in the leaves) and shorter upper leaf cells of B. acuta, but these gametophytic distinctions fail to consistently separate North American material from that of South America. In B. acuta the moist setae are erect to flexuous, while in B. magellanica Schimp. in C. Mull. they are cygneous. This distinction is quantitative; Frahm and Frey (1987) have shown that the structural basis for both setae types is the same; they differ only in the degree of asymmetrical thickening of the setal cells. Central American Blindia collections lack sporophytes, and so the name commonly associated with the taxon in Central America has been used.
Blindia acuta is separated from Dicranella and Ditrichum by its inflated, reddish yellow alar cells and from all other Central American members of the Dicranaceae with differentiated alar cells by its lack of internal costal differentiation.

**DITRICHACEAE**

Plants small to minute, gregarious or tufted, erect, simple, forked or cladocarpous. Leaves lanceolate, acuminate or subulate; costa single; cells short or elongate, smooth or mammillose. Perichaetia and sporophytes terminal; capsules exserted or immersed, stomata present or absent; annuli well-developed or absent; peristome present or absent.

**Key to the genera**

1. Upper leaf cells elongate to linear
   2
2. Leaves three-ranked
   6. Tristichium
3. Upper leaves in comal tufts; capsules immersed; calyptrae mitrate, mammillose
   5. Garckea
4. Ditrichum
4. Leaves distichous
3. Distichium
4. Leaves in many rows

5. Leaf apices obtuse; capsules immersed; peristome absent
   1. Bryomanginia

5. Leaf apices acute, acuminate or long setaceous; capsules exserted; peristome present
   6

6. Leaf apices acute to acuminate, margins strongly recurved, leaves not sheathing at base; capsules subinclined, furrowed when dry; peristome teeth deeply divided but united by trabeculae at the base
   2. Ceratodon

6. Leaf apices long setaceous, margins plane or weakly recurved, leaves sheathing at base; capsules erect, smooth when dry; peristome divided to the base
   4. Ditrichum


   Plants, small, densely tufted, reddish black, fastigiate branched; stem with the central strand poorly developed. Leaves oblong-linear; costa single, poorly differentiated in transverse section; cells incrassate, oval and bulging mammillose above, thin-walled and elongate below, basal marginal cells hyaline. Setae short; capsules cladocarpous, small, urn-shaped, immersed; stomata absent; annuli large, well-developed, persistent; peristome absent. Calyptrae cucullate. Spores bipolar, distally rugose.


Type. Peru, Cordillera Blanca, Cantuc Hirca, 31 May 1932, Lukas s.n.
Astomiopsis saint-pierrei Ther. ex Buck, Brittonia 31: 488. 1979, nom. illeg. inc. sp. prior.
Type. Mexico, Nevado de Toluca, Saint-Pierre 1780 (NY).

Bryomanginia saint-pierrei

Plants saxicolous; stems erect, to 1.5 cm long, fasciculate branched or branches arising below the vaginula. Leaves erect-spreading, oblong-lanceolate, concave, 1.5 mm long, apex obtuse; margins recurved from near the base to the apex, entire; costa percurrent, wide, filling the apex; upper laminal cells round to oval, 6-15 um | 6-8 um, incrassate, smooth to mammillose-bulging, bistratose at apex; basal cells rectangular, 75 um | 15 um, thin-walled, smooth; a few rows of cells extending upward along the margin as a short, hyaline border; alar cells not differentiated. Autoicous. Setae short, 0.3-0.5 mm long; capsules 0.5-0.6 mm long, smooth, light to dark brown; annuli of 1-3 rows of cells; opercula bluntly conic. Spores rounded, 25 um, distally rugose, brown.
Illustrations. Theriot (1931, Pl. 2); Herzog (1939, Figs. A-H as Melophyllum radiculosum); Bartram (1949, Fig. 11 A-E); Hegewald (1974, Figs. 1-8); Buck (1979, Figs. 1-8 as Astomiopsis saint-pierrei).

Habitat. On non-calcareous boulder; bare soil between clumps of tussock grasses.


World range: Mexico; Central America; Western South America.

An alpine species forming compact, dark greenish or reddish black cushions, *Bryomanginia saint-pierrei* is distinguished by its short, stout, obtuse, commonly bistratose leaves. In aspect it resembles ecostate members of *Andreaea*, but is more commonly found on soil rather than bare rock. It differs from the costate *Andreaea subulata* by its thin-walled basal leaf cells. From Central American members of the *Pottiaceae*, *B. saint-pierrei* is distinguished by the combination of its immersed capsules, well-developed annuli, smooth leaf cells, and costa that essentially lacks internal differentiation.

*Bryomanginia* can be confused with *Astomiopsis*, a genus with two species present in Mexico. According to Jerry Snider (pers. comm.), *Bryomanginia* has a tufted habit, fastigiate branches, bistratose leaves, mammillose-bulging upper leaf cells, basal cells forming a short hyaline margin, vesiculose cells both internally and externally in its annulus, and bipolar, distally rugose spores, while *Astomiopsis* has a loosely gregarious habit, simple branching, unistratose leaves, smooth leaf cells, undifferentiated basal margins, an annulus with thick-walled cells externally and vesiculose cells internally, and spherical, papillose-roughened spores.

Plants small, densely tufted; stems erect, simple or forked, densely foliate. Leaves ovate-lanceolate, gradually acuminate, acute, keeled; margins strongly reflexed to revolute, notched or irregularly serrulate near the apex; costa single, percurrent to short excurrent; cells smooth, elongate below, subquadrate above, thick-walled. Dioicous. Setae erect, elongate; capsules exserted, suberect; stomata present; annuli large, complex, revoluble; opercula conic; peristome single, teeth 16. Calyptrae cucullate.


Plants greenish yellow; secondary stems 2 cm long, branches sparse and irregularly spaced. Leaves crowded, curved and contorted when dry, ovate-lanceolate to lanceolate, 1.5-2 mm long; apex acute to acuminate; margins recurved nearly to the apex, coarsely and irregularly toothed; upper cells subquadrate to quadrate, 7-9 um long; basal cells short-rectangular; alar cells not differentiated. Setae 2 cm long, pale yellow to reddish, smooth; capsules suberect to inclined, ovoid-cylindrical, 2 mm long, yellow; urns sulcate when dry; stomata phaneroporic; opercula conic; peristome teeth reddish yellow, lanceolate, lightly papillose, split nearly to the base. Spores rounded, 11-15 um, finely papillose.

**Illustrations.** Grout (1936, Pl. 16 E); Bartram (1949, Fig. 12 D-F); Gangulee (1971, Fig. 94); Burley and Pritchard (1990, Pl. 3).

**Habitat.** On soil; 1981-3040 m.

**Distribution in Central America.** GUATEMALA. Chimaltenango: Standley 61909 (F, FH); Guatemala: Standley 80602 (F, FH); Huehuetenango: Standley 83092 (F, FH); Quezaltenango: Standley 85752 (F, FH); San Marcos: Steyermark 35787 (F, FH); Totonicapan: Standley 84551 (F, FH). EL SALVADOR. Santa Ana: Watson 110 (MO).

**HONDURAS.** Lempira: Allen 12247 (MO, TEFH). COSTA RICA. Alajuela: Alfaro 52 (FH, US); Cartago: Daly 1 (MO); Heredia: Tonduz 5597 (NY); San Jose: Crosby 3904 (MO). PANAMA. Bocas del Toro: Antonia 1673 (MO); Chiriqui: Croat 34842 (MO).

**World range:** Southwestern U.S.A., South-Central U.S.A.; Mexico; Central America; Caribbean, Northern and Western South America, Brazil; Southwestern and Southeastern Europe; China, Eastern Asia; Indian Subcontinent, Indo-China, Malesia; Macaronesia, Northern, Northeast Tropical, West-Central Tropical, East Tropical, and Southern Africa.
Ceratodon purpureus subsp. stenocarpus is separated from Ditrichum spp., by its keeled leaves and asymmetric, subinclined capsules that are variously furrowed when dry. It is distinguished from subsp. purpureus by its more erect, non-strumose, smooth to slightly furrowed capsules (inclined to horizontal, strumose and deeply furrowed in C. purpureus subsp. purpureus). Also in subsp. purpureus the peristome trabeculae are strongly thickened, and as a result the teeth are divided only 1/4 to 1/3 their lengths. In spp. stenocarpus the peristome teeth have weakly thickened trabeculae and are split nearly to the base. Burley and Pritchard (1990) demonstrated a morphological continuity between the two taxa by way of C. purpureus subsp. convolutus (Reichart) Burley.

Sterile C. purpureus has a pottiaceous look to it. Crum and Anderson (1981) emphasized the strongly reflexed to recurved leaf margins, irregularly notched apical serrulations, and the firm, smooth, subquadrate to quadrate upper cells of Ceratodon purpureus as aids in recognizing sterile collections.

Distichium capillaceum

1. Ditrichum ambiguum

Plants slender, elongate, densely tufted; stems erect, unbranched or forked. Leaves distichous, abruptly narrowed to a rough, spreading, linear subula from an oblong, erect, sheathing base; costa single, strong, filling the subula; cells subquadrate to subrectangular above, linear below; alar cells undifferentiated. Autoicous; perigonia axillary. Setae erect elongate; capsules exserted; annuli large, compound; opercula conic; stomata phaneroporic; peristome of 16 teeth. Calyptrae cucullate, smooth.


Plants green to yellow-green, 1-6 cm long. Leaves horizontally spreading, oblong-lanceolate, 3-5 mm long; margins erect, hyaline-bordered at base; upper laminal cells small, subquadrate to short rectangular, coarsely papillose; basal cells linear to oblong-linear, hyaline, smooth. Setae 8-20 mm long, red to reddish brown (occasionally yellowish); capsules erect to slightly inclined, cylindrical, 1-2 mm long, brown; peristome teeth lanceolate, split or perforate nearly to the base into 2 nearly equal divisions, papillose-roughened or smooth with oblique striations. Spores rounded, 16-25 um, papillose.

Illustrations. Grout (1903, Fig. 34); Bartram (1949, Fig. 12 A-C); Sainsbury (1955, Pl. 11 1); Smith (1978, Fig. 47 1-3); Gangulee (1971, Fig. 96); Magill (1981, Fig. 25 1-19); Crum and Anderson (1981, Fig. 58 A-D); Ireland (1982, Pl. 64 1-10); Noguchi (1987, Fig. 47); Matsui and Iwatuski (1990, Fig. 7).

Habitat. On rocks in forest; 3300 m.
Distribution in Central America. GUATEMALA. Huehuetenango: Standley 81627 (F, FH).
World range: Subarctic America, Western and Eastern Canada, Northwestern, North-Central, Northeastern, and Southwestern U.S.A.; Mexico; Central America; Western and Southern South America; Northern, Southwestern, Middle, East, and Southeastern Europe; Western Asia, Caucasus, Soviet Middle Asia, Siberia, Soviet Far
The distichous leaves and strongly clasping leaf bases of this species give the stems a smooth, flat appearance that may be mistaken for Fissidens, but the leaves lack vaginant laminae. The leaves are distinctive in their long, roughened, widely spreading subulae (more than twice the length of leaf base) that are abruptly contracted from sheathing, white bases.

A distichous habit is also found in Bryoxiphium (not yet known from Central America but present in Mexico) and Eustichium, but these genera have apiculate leaves. The only other Central American moss with strongly ranked leaves, Tristichium mirabile, has three-ranked, tightly appressed leaves that lack subulae.


Plants small to medium sized, loosely tufted, simple or sparsely branched. Leaves lanceolate or ovate-lanceolate, acuminate to setaceous, erect or clasping at base; costa single, strong, subpercurrent or excurrent; cells smooth; upper cells oval, quadrate to linear; lower cells rectangular to linear; alar cells undifferentiated. Setae elongate; capsules erect or inclined, cylindrical; annuli large, compound, frequently persistent; opercula conic or conic-rostrate; stomata present; peristome of 16 teeth split nearly to the base into 2 filiform, terete, divisions. Calyptrae cucullate, smooth, entire.

Ditrichum species in Central America have broad costae and may be confused with Campylopodiiella, which also has erect capsules and filiform peristome teeth. Campylopodiiella differs in having lax basal cells and a distinctive costal cross-sectional morphology (see discussion under that genus). The lax basal cells of Trematodon aid in separating sterile collections of it from Ditrichum. Without sporophytes Ditrichum is nearly inseparable from Dicranella. The tendency for some species of Dicranella to have subquadrate basal cells is the best means of recognizing sterile collections of Dicranella.
1. Leaf subula spirally twisted when dry, toothed at apex; cells at shoulders of leaf base quadrate to rounded-rectangular  

3. D. gracile

1. Leaf subula plane when dry, entire or serrulate at apex; cells long-rectangular to linear

2

2. Plants silky; leaves lance-subulate, lower leaf cells linear; autoicous; setae 12-25 mm long

2. D. difficile

2. Plants dull green; leaves lanceolate, gradually long acuminate, lower leaf cells long-rectangular; dioicous; setae 8-12 mm long

1. D. ambiguum


Plants small, 3-15 mm high, dull green to yellowish. Leaves 2.0-2.5 mm long, erect to erect-flexuous, with spreading points, ovate-lanceolate to lanceolate, subulate-acuminate; margins narrowly recurved, entire below, serrulate at apex; costa percurrent; cells firm-walled to incrassate; lower cells long-rectangular, 27-25 um long; upper cells short-rectangular, 15-17 um long. Dioicous. Setae 8-9 mm long, red; capsules erect, cylindric, 1.8-2.0 mm long; opercula high-conic, blunt; peristome teeth 500-800 um, split nearly to the base into 2 terete, filiform, red, densely spiculose, obliquely twisted divisions. Spores 12-13 um, smooth.
2. Ditrichum difficile

Illustrations. Bartram (1949, Fig. 14 A-D); Grout (1936, Pl. 29 B-C); Lawton (1971, Pl. 15 1-8); Crum and Anderson (1981, Fig. 53 I-O).

Habitat. On bank of bare soil; 1800-1900 m.


World range: Western Canada, Northeastern, Southeastern, Northwestern and Southwestern U.S.A.; Central America; Indian Subcontinent.

This species is recognized by its dioicous condition and rectangular to linear leaf cells. Central American material has longer leaf cells and more stiffly erect leaves than is typical for the species in North America; Crum and Anderson (1981) considered the Guatemalan material misnamed. All Central American material has the long, spiculose, obliquely twisted "tortuloid" peristome teeth that mark this species.


Plants slender, silky, densely tufted, yellowish green; stems 1-2 cm high, sparsely to densely tomentose. Leaves erect, flexuous, 2-3 mm long, lanceolate-subulate, from a
narrow subclasping base; margins erect to narrowly incurved, entire or faintly serrulate; costa percurrent to shortly excurrent with a few blunt teeth at the apex; cells firm-walled to incrassate, basal cells linear, 32-57 µm long, upper cells short-rectangular, 11-22 µm long. Autoicous. Setae 12-20 mm long, yellow becoming reddish with age; capsules erect to inclined, cylindric, 2.0 mm long; opercula conic-rostrate, 1 mm long, red; peristome teeth 0.5-0.6 mm long, divided nearly to the base into filiform, yellow or red, densely papillose, filiform divisions. Spores nearly smooth, 15 µm.

Illustrations. Bartram (1949, Fig. 11 F-H, as D. rufescens); Magill (1981, Fig. 24 1-9); Seppelt (1982, Fig. 10 1-17); Matsui and Iwatsuki (1990, Fig. 16).

Habitat. On bare soil, soil over rocks and as an epiphyte; 1800-3200 m.

Distribution in Central America. GUATEMALA. Huehuetenango: Sharp 4950 (FH); Quiche: Sharp 5307 (F, FH). HONDURAS. Cortes: Allen 14048 (MO, TEFH); Lempira: Allen 12121 (MO, TEFH); Morazan: Allen 12399 (MO, TEFH); Olancho: Allen 12486 (MO, TEFH). COSTA RICA. Puntarenas: Gomez et al. 21775 (MO).

PANAMA. Bocas del Toro: Gomez et al. 22494 (MO).

World range: Mexico; Central America; Caribbean, Western, Northern and Southern South America, Brazil; China, Eastern Asia, Soviet Far East; Indian Subcontinent, Malesia; East Tropical and Southern Africa, Madagascar; Australia, New Zealand; Southwestern Pacific.

Ditrichum difficile is recognized by its slender, silky appearance, autoicous condition, and elongate leaf cells. Central American material, commonly known in the West Indies, Central and South America as Ditrichum rufescens, differs in no way from South African material of Ditrichum difficile, a widespread Southern Hemispheric moss.
Ditrichum steyermarkii Bartr., Bryologist 49: 110. 1946. Type. Guatemala, San Marcos, between San Sebastian at km 21 and km 8, Steyermark 35657 (F, FH), syn. nov.

Plants slender, in tall or short tufts, yellowish green to reddish yellow, 2-10 cm tall, sparsely to densely radiculose below. Leaves erect, sub-erect or laxly spreading with points often spirally twisted when dry, 4-8 mm long, abruptly or gradually linear-subulate from a clasping base; costa long excurrent, variously thickened, 50-80 um wide, toothed at apex; cells thickened with pellucid walls; basal cells extremely variable in shape, linear to rectangular, 17-55 um long, interior cells pitted or smooth, marginal cells at extreme base thin-walled, hyaline, forming an indistinct border, cells at the apex of the sheathing base irregularly oval to quadrate. Sporophyte not known in Central America.

Illustrations. Bartram (1949, Figs. 12 G-I, 13 A-J, as D. longicaule, D. giganteum and D. steyermarkii); Frisvoll (1985, Figs. 15-21); Matsui and Iwatsuki (1990, Fig. 13, as D. crispatissimum).

Habitat. On soil, rocks and on trees; 3300-4600 m.
Distribution in Central America. GUATEMALA. Chimaltenango: Kellerman s.n. (FH, US); Huehuetenango: Standley 83087 (F, FH, MO, US); San Marcos: Steyermark 35514 (F, FH); Solola: Steyermark 47497 (F, FH, MO, US).
World range: Subarctic America, Western and Eastern Canada, Northwestern and North-Central U.S.A.; Central America; Western South America; Northern,
Southwestern, Middle, East, and Southeastern Europe; Soviet Middle Asia, Siberia, China, Eastern Asia; Malesia; New Zealand.

In this species the leaves are clasping at base with a linear, setaceous subula that is filled by the long excurrent costa. The subula is toothed at the apex and commonly, but not always, spirally twisted when dry. The cells in the clasping leaf base are of two forms, long rectangular to linear below and irregularly oval to subquadrate above. This species represents an intergrading complex with three expressions in Central America. The expressions differ quantitatively in four features: plant size; subula length, width and twisting; leaf base width; and ratio of lower cell form to upper cell form. In D. gracile plants are medium sized with stiff, erect leaves, long, broad, distinctly twisted subulae, wide leaf bases, and equally divided leaf cell ratios. In D. crispatissimum plants are robust with erect-splaying leaves, the subulae are medium length, very narrow and moderately twisted, the leaf base is narrow, and most of the leaf cells are of the lower cell form. In D. longicaule plants are small, with stiffly falcate leaves, short, broad and weakly twisted subulae, an intermediate sized leaf base, and cells mostly of the upper cell form.

The few Central American collections of this taxon can be sorted into the above expressions, but these taxa are here treated as a single complex because of their relationship to two other widespread, extremely variable species, D. punctulatum Mitt. and D. flexicaule (Schwaegr.) Hampe. The problem has been partially treated by Seppelt (1982) and Frisvoll (1985), but their conclusions are contradictory. It may be that this complex represents a single, extremely variable and widespread taxon.


Plants very small, gregarious, loosely tufted, dull yellowish green or brownish; stems erect, simple. Leaves small below, upper leaves in comal tufts; costa single, strong; upper leaf cells linear, smooth, firm-walled; basal cells broader, thin-walled. Dioicous. Setae short; capsules immersed; annuli large, compound; opercula conic, short beaked; stomata absent; peristome teeth 16. Calyptrae conic-mitracte, coarsely mammillose.


Garckea phascoides C. Mull., Bot. Zeitung (Berlin) 3: 865. 1845. Type. Java, insula ubi in
provincia Buitenzorg.


Plants 5-10 mm high, terricolous. Leaves erect-speading, loosely appressed, lanceolate-acuminate, 2 mm long, apex bluntly acute; margins plane, slightly spinose-sinuate in upper half; costa subpercurrent, minutely papillose, in transverse section with guide cells and ventral stereids well-developed; upper cells linear 35-75 um | 3-5 um, incrassate, bistratose in parts, smooth; basal cells broader and laxer, alar cells not differentiated. Setae 0.5 mm long, red; capsules ovate-cylindrical, 1 mm long; peristome teeth lanceolate, strongly articulate below, entire, fenestrate or irregularly divided into forks, densely papillose, the papillae in vertical lines. Calyptrae 0.4 mm long. Spores 17-20 um, finely papillose.

Illustrations. Hooker (1829, Pl. 21 l-11, as Dicranum phascoides); Dozy and Molkenboer (1845, Tab. 59, as Garckea phascoides); Fleischer, (1904, Fig. 45, as Garckea phascoides); Brotherus (1909, Fig. 173 A-E, as Garckea phascoides); Brotherus (1924, Fig. 133 A-E, as Garckea phascoides); Crum (1953, Figs. 1-9 as G. phascoides); Gangulee (1971, Fig. 82, as G. phascoides); Noguchi (1987, Fig. 41 B).

Habitat. On shady clay roadbank.

Distribution in Central America. PANAMA. Chiriqui: Llano (FH).

World range: Central America; Brazil; China, Eastern Asia; Indian Subcontinent, Indo-China, Malesia; Madagascar; Australia; Northwestern Pacific.

This is a weedy, widespread moss in southern Asia. Gametophytically it resembles the long-celled species of Ditrichum or Dicranella, but the upper leaves are crowded /-----------------------------\
Garckeia flexuosa  Tristichium mirabile

into comal tufts. It is the only Central American species of Ditrichaceae with mitrate calyptrae. It shares with Bryomanginia saint-pierrei an immersed capsule, but that species occurs in dense reddish brown tufts, has obtuse leaves, rounded, thick-walled leaf cells, and is eperistomate. The nomenclatural tangle surrounding this species has been worked out by Margadant and Norkett (1973).


Plants small, slender. Leaves appressed, three-ranked, strongly concave or keeled; costa single, strong, subpercurrent; cells elongate throughout, firm-walled, alar cells not differentiated. Autoicous. Setae short; capsules exserted; annuli simple; peristome absent. Calyptrae cucullate.


Plants scattered, green to yellow-green, terricolous; stems 10-15 mm long, simple or irregularly branched. Leaves 0.8-1.2 mm long, keeled, narrowly lanceolate,
gradually tapered from base; apex bluntly acute; margins erect, entire; cells linear, 37 um | 5 um, incrassate, smooth. Gonioautoicous. Setae to 4 mm long, brownish yellow, smooth; capsules inclined, ovoid, 1 mm long; annuli revoluble; opercula short-rostrate, 0.5 mm long; stomata absent. Spores spherical, 20-25 um, lightly papillose, brown.

Illustrations. Magill (1981, Fig. 26 1-14); Herzog (1916, Fig. 2, 4 A-C).
Habitat. On soil; 3300-3600 m.
Distribution in Central America. COSTA RICA. San Jose: Bowers 849d (MO). World range: Mexico; Central America; Northern and Western South America; Southern Africa.

Tristichium mirabile has closely appressed, tristichous leaves. The leaves may appear two-ranked (when plants are young, branched or have perichaetia), causing some confusion with Eustichia or Bryoxiphium, but those genera have subquadrate leaf cells. Distichium capillaceum and Conostomum tetragonum also have flattened, appressed leaves. In D. capillaceum the leaves are abruptly contracted to long, roughened subulae, while C. tetragonum has four-ranked, less tightly appressed leaves.

FISSIDENTACEAE
by Ronald A. Pursell

Plants aquatic, lignicolous, saxicolous, or terrestrial, small to large, 1 mm to 8 cm or more in length, unbranched or branched; stem with or without a central strand; axillary hyaline nodules present or absent; rhizoids basal or axillary, smooth or papillose. Leaves distichous and equitant, each differentiated into two vaginant laminae that clasp the stem, a dorsal lamina and a ventral lamina; costa single (nearly lacking in a few species), ending well below the leaf apex to excurrent; cells 1(2)-stratose (multistratose in a few species), irregularly hexagonal to rounded, isodiametric to elongate, sometimes guttulate (small, clear, drop-like areas in cells), smooth, mamilllose, unipapillose or pluripapillose, sometimes much elongated and thick-walled at the margins (infrequently submarginal) and forming uni- to multistratose limbidia on all laminae or portions thereof. Monoicous, synoicous or dioicous; perichaetial and perigonial leaves often differentiated; paraphyses lacking. Sporophytes terminal on
stems and branches, often appearing lateral or basal, 1(-2, infrequently more) per perichaetium. Setae mostly elongate (immersed to very short in some species of subgenera Octodiceras and Sarawakia); capsules erect or inclined, symmetric to somewhat arcuate; annuli none; peristome haplolepideous (absent in a few species), teeth typically divided to below the middle, sometimes divided irregularly or undivided, red to red-brown, spirally thickened or articulate above, smooth to papillose to striolate or ridged below; opercula conic to long-rostrate from a conic base. Spores smooth to finely papillose. Calyptrae cucullate or mitrate, smooth or papillose.

The family consists of a single genus, Fissidens Hedw., six subgenera, and approximately 500 species worldwide. Not all subgenera are represented in Central America. Fissidens hyalinus, F. juruensis var. juruensis, and F. cylindraceus have not been reported from Central America, but are included in the key since they are likely to be encountered.

1. Leaves ecostate or nearly so  [F. hyalinus]

1. Leaves costate

2. Plants aquatic

3. Plants rigid and firm or flexuous, not feathery in appearance; leaves lanceolate to oblong-lanceolate; laminal cells irregularly bistratose or bi- to multi-stratose

15. F. fontanus

3. Plants often feathery in appearance; leaves linear-lanceolate; laminal cells unistratose

4. Leaves limbate, limbidium more or less cartilaginous; laminal cells irregularly
bistratose; plants flexuous

4. Leaves elimbate; laminal cells bi- to multi-stratose; plants rigid and firm
   18. F. grandifrons

5. Leaves (1.8-)2.5-3.5(-4.5) mm long; dorsal lamina limbidium (16-)25-54(-62) um wide at middle, (2-)4-5(-9) cells thick
   38. F. rigidulus

5. Leaves 1.3-2.2 mm long; dorsal lamina limbidium (9-)13-16(-22) um wide at middle, 1-3 cells thick
   3. F. anguste-limbatus

6. Laminal cells pluripapillose, often indistinctly so
   39. F. scariosus

6. Laminal cells smooth, bulging, mammillose or unipapillose
   7

7. Laminal cells smooth, elongate-prosenchymatous

7. Laminal cells smooth, mammillose or unipapillose, not prosenchymatous
   8

8. Laminal cells mostly longer than 18 um, smooth, thin-walled, shrunken when dry
   Key B

8. Laminal cells less than 18 um, smooth, mammillose or unipapillose, thin- to thick-walled, firm, not greatly shrunken when dry
   9

9. Leaves elimbate
   Key C

9. Leaves limbate on all laminae or only on the vaginant laminae
   Key A

   Key A. Fissidens with leaves limbate; laminal cells smooth, bulging, mammillose or unipapillose

1. Limbidium on all laminae of a leaf; guttulae not present
   2

1. Limbidium more or less confined to the vaginant laminae; guttulae often present
2. Juxtacostal cells in basal half of vaginant laminae greatly enlarged, oblong, smooth, and mostly pellucid

3. Laminal cells smooth to bulging

4. Dorsal lamina elimbate at base, marginal cells crenulate; costa percurrent to ending 4-5 cells below leaf apex

5. Costa percurrent to short-excurrent

6. Limbidium thick and cartilaginous, (16-)25-54(-62) um wide and (2-)4-5(-9) cells thick; laminal cells irregularly 2-stratose, 5-9 um long

7. Limbidium narrow, to 23 um wide and 1-3 cells thick; laminal cells unistratose, 8-10 um long
7. Plants aquatic or subject to inundation; laminal cells more or less quadrate in cross section; axillary hyaline nodules absent

8

7. Plants in dry or drier habitats; laminal cells usually more or less twice as thick as wide in cross section, infrequently quadrate; axillary hyaline nodules present or absent

9

8. Leaves more or less ovate; vaginant laminae 2/3 leaf length; limbidium reaching leaf apex or ending just below it

3. F. angustelimbatus

8. Leaves more or less lanceolate; vaginant laminae 1/2 leaf length; limbidium ending well below leaf apex

7. F. bryoides var. pusillus

9. Limbidium of vaginant laminae more or less dentate

44. F. wallisii

9. Limbidium of vaginant laminae more or less entire

10

10. Perichaetial stems usually much shorter than infertile stems; limbidium confluent with short excurrent costa

9. F. curvatus

10. Perichaetial and infertile stems not noticeably different in size; limbidium usually ending below apex; costa percurrent to excurrent

11

11. Laminal cells bulging, infrequently smooth; axillary hyaline nodules present

8. F. crispus

11. Laminal cells unipapillose; axillary hyaline nodules absent

17. F. goyazensis
12. Limbidium confined to perichaetial leaves and subtending upper leaves (often inconspicuous) or absent
   13
12. Limbidium on all or most leaves
   17
13. Laminal cells unipapillose; guttulae lacking
   14
13. Laminal cells smooth; guttulae often present
   15
14. Laminal cells more or less sharply unipapillose
   11. F. diplodus var. wainionis
   14. Laminal cells with long, often forked papillae

10. F. diplodus var. diplodus
15. Costa percurrent to excurrent
   16
15. Costa usually ending 2 or more cells below the leaf apex
   32. F. pellucidus
16. Marginal cells conspicuously smaller than inner laminal cells; costa long-excurrent
   29. F. ornatus
16. Marginal cells not conspicuously smaller than inner laminal cells; costa ending below the leaf apex to short-excurrent
   32. F. pellucidus
17. Cells smooth; guttulae present  
24. F. leptophyllus

17. Cells unipapillose; guttulae absent

18. Limbidium extending to apices of vaginant laminae, often onto the adjacent ventral laminae
21. F. intermedius

18. Limbidium not extending more than 0.75 the length of the vaginant laminae
19

19. Vaginant laminae very broad, appearing to encircle the stem, margins recurved
40. F. sharpii

19. Vaginant laminae neither broad nor encircling the stem, margins not recurved
20. F. hornschuchii

Key B. Fissidens with leaves variably limbate; laminal cells large, thin-walled, greatly shrunken when dry and often difficult to revive

1. Leaves limbate only on vaginant laminae; limbidia weak and inconspicuous
2

1. Leaves limbate on all laminae; limbidia conspicuous
3

2. Costa ending far below the leaf apex
[F. juruensis var. juruensis]
2. Costa percurrent
23. F. juruensis var. percurrents

3. Limbidium 3-4-stratose, confluent at leaf apex; leaves to about 5.5 mm long
27. F. mollis

3. Limbidium bi-stratose, ending below leaf apex; leaves generally less than 3 mm long
4

4. Laminal cells (13-)18-27(-32) um long by 9-14 um wide, quadrate to oblong, pentagonal and hexagonal
12. F. dissitifolius
4. Laminal cells (16-23-26-48) μm long by (7-13-18-20) μm wide, mostly oblong-hexagonal

37. F. reticulosus

Key C. Fissidens with leaves elimbate; laminal cells smooth, bulging, mammillose or unipapillose

1. Cells on all or some laminae mammillose or unipapillose

2. All laminal cells smooth or bulging

4

2. All laminal cells sharply unipapillose; leaf margins serrulate, often coarsely dentate on vaginant laminae

31. F. papillosus

2. Vaginant laminal cells mammillose, other laminal cells either smooth or mammillose; leaf margins crenulate

3

3. Ventral and dorsal laminal cells bulging or smooth; costa ending in a stout cuspidate leaf apex; setae basal; plants often 10 mm or more in length

43. F. taxifolius

3. Ventral and dorsal laminal cells mammillose; costa ending at or below the leaf apices; sporophytes unknown; plants usually no more than 8 mm long

41. F. steerei
4. Plants small, usually no more than 5 mm long  
5
4. Plants large, at least 10 mm long, usually longer  
12

5. Juxtacostal cells in base of vaginant laminae conspicuously enlarged, oblong and more or less pellucid  
33. F. platyphyllus
5. Juxtacostal cells in base of vaginant laminae neither noticeably enlarged, oblong, nor pellucid  
6

6. Upper leaf cells convex-thickened; apical end of costa with 2 rows of guide cells; guttulae absent  
7
6. Upper leaf cells evenly thickened or mammillose; apical end of costa with 1 row of guide cells; guttulae present or absent  
8

7. Leaves mostly broadly acute or rounded-obtuse and caducous; peristome reduced  
36 F. radicans
7. Leaves abruptly narrowed to rounded-obtuse apices, persistent; peristome complete  
1. F. allenianus

8. Costa conspicuous, occupying 1/3 or more of the leaf width; laminal cells bulging, irregularly bistratose; guttulae absent  
2. F. allionii
8. Costa strong but occupying less than 1/3 the leaf width; laminal cells smooth to bulging, unistratose or irregularly bistratose; guttulae present or absent  
9

9. Costae excurrent to long excurrent  
11
9. Costae percurrent or ending 2 or more cells below leaf apex  
10

10. Marginal 2-4 rows of cells lighter in color than the inner laminal cells; guttulae absent; perichaetia lateral, near base
13. F. dubius
10. Marginal cells not different in color from inner laminal cells; guttulae usually present; perichaetia terminal
32. F. pellucidus

11. Marginal 1-3 rows of dorsal and ventral laminal cells conspicuously smaller than inner cells; dorsal lamina usually ending at insertion
29. F. ornatus
11. Marginal cells of dorsal and ventral laminae not conspicuously smaller than inner cells; dorsal lamina usually ending well above insertion
42. F. subulatus

12. Marginal 3-5 rows of dorsal and ventral laminal cells usually darker than inner cells; inner laminal cells irregularly bistratose
6. F. bourgaeanus
12. Marginal dorsal and ventral laminal cells neither darker nor lighter; laminal cells unistratose
13

13. Upper laminal cells 7.5-12 um long, outer walls convex-bulging
5. F. asplenioides
13. Upper laminal cells 15-16 um long, outer walls flat
35. F. polypodioides

Key D. Fissidens with laminal cells pluripapillose; leaves limbate or elimbate

1. Leaves elimbate
2
1. Leaves limbate
4
2. Leaf apex rounded-acute to obtuse, not ending in a clear sharp cell; costa very short to subpercurrent

3

2. Leaf apex acute, most ending in a clear sharp cell; costa subpercurrent to short-excurrent

14. F. elegans

3. Vaginant laminae of all leaves unequal, minor lamina narrowed above and ending on or very near the costa; costa very short, often not extending much beyond vaginant laminae

16. F. gardneri

3. Vaginant laminae nearly equal, except those of perichaetial leaves; costa usually ending 3 or more cells below leaf apex

26. F. minutus var. pusillissimus

4. Limbidium unistratose

5

4. Limbidium 2-4 stratose

17

5. Limbidium extending the complete length of the vaginant laminae or nearly so

6

5. Limbidium not exceeding 3/4 the length of the vaginant laminae

7

6. Limbidium strong, typically extending a short distance onto the adjacent ventral laminae, present on all leaves of perichaetial and sterile stems except scale-like basal ones; costa percurrent to short-excurrent

22. F. intramarginatus

6. Limbidium weak, 1-2(-3) cells wide, not extending onto the adjacent ventral lamina, not necessarily present on all leaves of perichaetial and sterile stems; costa subpercurrent to percurrent
14. F. elegans

7. Limbidium marginal

8. Limbidium intralaminal for at least part of their length

13

9. Leaves obtuse or narrowed abruptly to short, rounded apices

19. F. guianensis

10. Vaginant laminae conspicuously unequal, minor lamina usually ending on or very near the costa; limbidium restricted to perichaetial leaves, indistinct

16. F. gardneri

11. Costa ending 3-8(-16) cells below leaf apex (infrequently percurrent); peristome teeth divided more or less 2/3 their length, strongly inflexed when wet

12

11. Costa ending 2-5 cells below leaf apex; peristome teeth divided nearly their entire length, erect wet or dry

[F. cylindraceus]

12. Leaves 0.5-1.2 mm long; stems to 8.5 mm long; limbidium usually distinct

25. F. minutus var. minutus
12. Leaves 0.4-0.8 mm long; stems to 2 mm long; limbidium often indistinct
   26. F. minutus var. pusillissimus

13. Limbidium confined to perichaetial and subtending leaves
   14
13. Limbidium on leaves of perichaetial and sterile stems
   16

14. Leaves rounded or rounded-acute; costa ending below leaf apex
   15
14. Leaves acute, each ending in a clear, sharp cell; costa ending below leaf apex to short-excurrent
   14. F. elegans

15. Leaves 0.5-1.2 mm long; stems to 8.5 mm long
   25. F. minutus var. minutus
15. Leaves 0.4-0.8 mm long; stems to 2 mm long
   26. F. minutus var. pusillissimus

16. Leaves usually tapering to short rounded apices; costa ending below apices
   28. F. neglectus
16. Leaves acute, each ending in sharp clear cells; costa ending below leaf apices to short-excurrent
   14. F. elegans

17. Limbidium on all laminae of nearly all leaves
   18
17. Limbidium confined to vaginant laminae and the adjoining part of ventral laminae
   46. F. weirii var. hemicraspedophyllus

18. Limbidium confluent at apex of leaves; sporophytes 1-6 per perichaetium
   34. F. plurisetus
18. Limbidium ending below leaf apex; sporophytes 1-2 per perichaetium
   19

19. Limbidium marginal
   45. F. weirii var. weirii
19. Limbidium intramarginal on dorsal and ventral laminae
47. F. weirii var. insertus

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1. Fissidens allenianus                2. Fissidens allionii

   Type. U.S.A., Florida, Pursell 2915 (PAC, U).

   Plants to 7.5 m | 1.5-2.5 mm | 0.3-0.4 mm; apex abruptly narrowed, rounded-obtuse; margins crenulate; vaginant laminae 1/2-2/3 the leaf length, somewhat unequal; minor laminae acute-rounded; costa ending (4-)5-7(-10) cells below the apex, 2 stereid bands distally, 3 stereid bands proximally; cells smooth. Sporophytes terminal.

   Illustrations. Bruggeman-Nannenga and Pursell (1990, Figs. 1-10).
   Habitat. Mainly corticolous but also found on limestone; sea level to 600 m. Distribution in Central America. BELIZE. Belize: Robertson s.n. (NY); Corozal: Balick et al. 2206 (NY). GUATEMALA. Peten: Lundell 3337 (FH).
   World range: Southeastern U.S.A.; Mexico; Central America; Caribbean.
Fissidens allianianus, recently recognized as distinct from F. radicans, differs from the latter species in having persistent leaves with mostly abruptly narrowed apices, dorsal laminae ending above the insertion, and a complete peristome. In F. radicans the cauducous leaves are mostly broadly acute to rounded-obtuse, the dorsal laminae end at or very near the insertion, and the peristome is reduced.


Plants 4.0-5.55 mm | 1.5-1.75 mm. Leaves to 1.5 mm | 0.15-0.18 mm; apex acute; margins serrulate to more or less entire; vaginant laminae more or less 1/2 the leaf length, unequal; minor laminae acute; costa very strong, (31-)36-50-(54) um broad, occupying 1/2 or more the width of the leaves, excurrent; cells 6-9 um in diameter, more or less sharply mammillose-papillose, bistratose in places. Sporophytes terminal on short axillary branches.

Illustrations. None

Habitat. Usually on bare soil; 300 m.

Distribution in Central America. PANAMA. Darien: Allen 8931 (MO).

World range: Central America; Western and Northern South America, Brazil.

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3. Fissidens anguste-limbatus  

Fissidens allionii, one of the easiest species in the local flora to identify, is recognized by its large percurrent to short-excurrent costa that occupies 1/2 or more the width of the narrow leaf. Moreover, the leaves are tightly imbricate and the mammillose laminal cells are bistratose in places.


Plants 8-40 mm | 1.5-3 mm. Leaves 1.3-2.2 mm | 0.4-0.6 mm; apex obtuse to more or less rounded, usually mucronate; margins limbate, more or less entire, 2-3 stratose; vaginant laminae 0.66-0.75 the leaf length, equal; costa percurrent to short-excurrent; cells 8-13 um | 6-10 um, smooth, flat to slightly bulging, irregularly quadrate to oblong and irregularly hexagonal. Sporophytes terminal.

Illustrations. Florschutz (1964, Fig. 11 A-D, as F. pennula); Bruggeman-Nannenga (1973, Fig. 1 A-D, as F. smaragdinus, Fig. 2 A-D, as F. capillisetoides, Fig. 4 A-F, as F. pennula, Fig. 5 A-E, as F. goebelii, Fig. 6 A-D, as F. variabilis).

Habitat. On rocks in streams and along margins of streams at low elevations to about 1000 m.
Distribution in Central America. PANAMA. Chiriqui: Salazar et al. 713 (PMA).
World range: Central America; Northern and Southern South America, Brazil.

Fissidens anguste-limbatus can be confused with F. crispus, but, while the former is aquatic, the latter occurs on soil, tree trunks or moist rocks. Moreover, the laminal cells in F. anguste-limbatus are more or less flat and in section are about as deep as
they are wide. Conversely, the laminal cells of F. crispus are strongly bulging and usually twice as thick as wide.


Plants (2-)3-5(-8) mm | to ca. 3 mm. Leaves 1.5-2.5 mm | 0.2-0.3 mm; apex acute to broadly acute; margins limbate, more or less entire, serrulate at apices; vaginant laminae more or less 1/2 the leaf length, equal, acute; costa (20-)23-30(-33) um broad, percurrent to short-excurrent; cells (8-)10-13(-15) um in diameter, mammilllose-papillose, irregularly hexagonal, those juxtacostally in parts of proximal vaginant laminae large, more or less oblong and pellucid. Sporophytes terminal.

Illustrations. None.
Habitat. On soil at low elevations.
World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil; Southwestern Pacific.

Fissidens angustifolius is one of four neotropical species (along with F. panamensis, F. yucatanensis, and F. goyazensis) with completely limbate leaves and unipapillose cells. It differs from the first two by its costa percurrent to short-excurrent and limbidium that descends to the base of the dorsal laminae. In both F. panamensis and F. yucatanensis the proximal part of the dorsal lamina is edged with hyaline crenulate
cells, and the costa usually ends short of the leaf apex, often by several cells in the former species. Fissidens angustifolius differs further from F. yucatanensis by its smaller leaf cells (10-13 um vs. 12-18 um). Fissidens goyazensis has more or less homogeneous vaginant laminal cells and as such differs from the other three species, which have enlarged, oblong and pellucid cells in the lower half of the vaginant laminae.


Plants to 5 cm | ca. 4 mm. Leaves 2.0-2.5 mm | 0.3-0.4 mm; apex rounded-obtuse and apiculate; margins crenulate; vaginant laminae more or less 3/4 the leaf length, unequal; minor laminae mostly rounded and more or less free distally; costa ending several cells below the apex; cells 8-10 um long, smooth, convexly thickened. Sporophytes terminal.

Illustrations. Hedwig (1801, Pl. 28); Grout (1943, Pl. 8 112-120); Bartram (1949, Fig. 8 F-H); Crum and Anderson (1965, Figs. 1, 3, 5-6, 9-10, 13-14, 16); Crum and Anderson (1981, Fig. 32 D-H).

Habitat. Usually found on soil; 1200 m or above.
Distribution in Central America. GUATEMALA. Baja Verapaz: Sharp 2651 (FH); Chimaltenango: Richards et al. 2885 (PAC); Chiquimula: Steyermark 30922 (NY); El Progreso: Sharp 2717a (FH); Quezaltenango: Sharp 2284 (FH, PAC, TENN); Quiche: Richards 2937 (PAC); Sacatepequez: Standley 58957 (FH); San Marcos: Steyermark 36488 (FH); Solola: Richards et al. 3044 (MO, NY, PAC); Zacapa: Steyermark 43204 (MO). EL SALVADOR. Ahuachapan: Standley & Padilla 2589 (FH). HONDURAS. Comayagua: Allen 11798 (MO, TEFH); Cortes: Allen 14131 (MO); Lempira: Allen 11153 (MO, TEFH); Morazan: Allen 12374 (MO, TEFH); Olancho: Allen 12531 (MO, TEFH). COSTA RICA. Alajuela: Crosby 3612 (MO); Cartago: Crosby 10884 (MO, PAC); Heredia: Crosby 6580 (MO, PAC); Puntarenas: Crosby 2534 (MO); San Jose:
Crosby 6210 (MO, PAC). PANAMA. Bocas del Toro: Allen 5045 (MO, PAC); Cocle: Salazar et al. 953 (PAC, PMA); Chiriqui: Allen 9174 (MO, PAC); Panama: Salazar & Belize 943 (PAC, PMA).

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5. Fissidens aspleniodes               6. Fissidens bourgaeanus

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean, Western, Northern, and Southern South America, Brazil; Macaronesia, West Tropical, West-Central Tropical, East Tropical and Southern Africa, Western Indian Ocean; Indian Subcontinent, Indo-China, Malesia; Australia, New Zealand.

Fissidens asplenioides is the largest moss in Central America belonging to section Amblyothallia C. Mull. (which is recognized by its three stereid bands in the lower half of the costa and convexly thickened upper laminal cells). Plants often approach 5 cm in length with leaves that are nearly 4 mm long. Upon drying, the lanceolate to lingulate leaves commonly curl tightly inward from the tips. Often re-moistened material will not lie flat when preparations for examination are made.

This species is the only Central American representative of the section with a
rounded minor lamina that is more or less free at its distal end. The minor lamina may be to 3/4 the leaf length. In addition, the marginal cells of the vaginant laminae are narrow, somewhat elongate and with the long axis obliquely to vertically oriented.


   Plants to 6.5 cm | 10 mm. Leaves 3.4-6.2 mm | 0.5-1.3 mm; apex acute to short-acuminate; margins elimbate, entire to irregularly dentate at apex, more or less entire to irregularly serrate on the vaginant laminae; vaginant laminae 0.5-0.6 the leaf length, equal to slightly unequal, acute; costa percurrent; cells (8-)10-12(-15) um long, occasionally irregularly bistratose, smooth to slightly bulging, rounded to irregularly hexagonal, 3-5 marginal rows thicker, forming a darker marginal band. Sporophytes unknown, male branches short, axillary.

   Illustrations. Grout (1943, Pl. 9 127, 128); Bartram (1949, Fig. 8 F-H).
   Habitat. On soil, limestone, or epiphytically; 1500 m or above.
   Distribution in Central America. GUATEMALA. Alta Verapaz: Standley 89819 (FH); Huehuetenango: Steyermark 48575a (FH, NY); Quiche: Sharp 2405b (FH, PAC, TENN). HONDURAS. Olancho: Allen 11646 (MO); Santa Barbara: Allen 11619 (MO).
   World range: Mexico; Central America; Caribbean.

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Fissidens bourgaeanus is the largest member (plants to 5 cm long) of subgenus Serridium C. Mull. in Central America. The laminal cells, usually unistratose, are occasionally irregularly bifastate. The marginal three to five rows of laminal cells are usually thicker than the inner cells, and as a result the leaves usually have a darker marginal band. Less frequently the border can be as light as that seen in F. dubius. However, even in this case the outer cells (in section) are somewhat thicker than the inner laminal cells. In F. dubius the marginal cells are not thicker (usually thinner) than the inner laminal cells. The leaf margins can be nearly entire throughout or irregularly dentate in the apices and entire, serrate, or serrulate on the vaginant laminae. Sporophytes of this species are unknown.

The nearest relative of F. bourgaeanus appears to be the Hawaiian F. pacificus Angstr.


Plants 3–9 mm | ca. 1.5 mm. Leaves 0.7–2 mm | 0.2–0.3 mm; apex obtuse to broadly acute; margins limbate, more or less entire, limbidium ceasing below the apex and above base of dorsal laminae; vaginant laminae more or less 1/2 the leaf length, unequal, acute; costa ceasing a few cells below apex; cells irregularly quadrate to irregularly hexagonal, (6–)8–10(-13) µm long, smooth to slightly bulging. Sporophytes terminal.

Illustrations. Bruggeman-Nannenga (1982, Fig. 5 a–c, f); Crum and Anderson
Habitat. On silicious rocks and limestone along streams; ca. 900 m.
Distribution in Central America. HONDURAS. Comayagua: Allen 11746 (MO);
Cortes: Allen 14387 (MO); Olancho: Allen 12802 p.p. (MO). PANAMA. Chiriqui:
Salazar et al. 5140 (PAC, PMA).
World range: North-Central, Northeastern, South-Central, and Southeastern
U.S.A.; Mexico; Central America; Northern, Southwestern, Middle, Southeastern, and
East Europe; Japan.

Fissidens bryoides, sensu lato, consists of a number of intergrading expressions.
The variety pusillus is one of these and is recognized by its more or less aquatic habitat
and obtuse leaves with costa and limbidium that ends below the apex. The limbidium
ends above the leaf insertion and in the lower leaves is often lacking from the ventral
and dorsal laminae.

d'Orbigny (FH).
1892. Type. Costa Rica, Polakowsky (FH, NY).

Fissidens longidecurrens Ther., Smithsonian Misc. Collect. 78: 10. 1926. Type. Mexico,
Arsene 4892 (US).

Plants to 35 mm | 3 mm. Leaves to 2.2 mm | 0.2-0.5 mm; apex acute to obtuse
and apiculate; margins more or less entire, denticulate at leaf apices, limbate on all
laminae, limbidia 2-stratose; vaginant laminae more or less equal, acute, 2/3-3/4 the
leaf length; costa ending 1-3 cells below the apex, occasionally short excurrent; cells
6-10 um, smooth but bulging, irregularly hexagonal. Sporophytes terminal.

Illustrations. Bartram (1949, Fig. 4 C-E; Fig. 4 A-B, as F. longidecurrens).
Habitat. On shaded soil, tree trunks and moist rocks at moderate to high elevations.
Distribution in Central America. GUATEMALA. Alta Verapaz: Standley 70469 (FH, NY); Chimaltenango: Godman & Salvin (FH); El Progreso: Sharp 2717 (FH); Escuintla: Holdridge (MICH); Huehuetenango: Steyermark 50457 (FH, MICH, NY); Quezaltenango: Steyermark 34092a (FH); Quiche: Richards et al. 2950 (PAC); Sacatepequez: Williams 43539 (PAC); San Marcos: Sharp 5471 (FH); Solola: Richards et al. 2922 (PAC); Zacapa: Steyermark 29452 (FH, MICH). EL SALVADOR. La Libertad: Chapman B-21 (MICH); Santa Ana: Watson 83 (MO). HONDURAS. Comayagua: Allen 11052 (MO, TEFH); Lempira: Allen 11403 (MO, TEFH); Morazan: Allen 12393 (MO, TEFH); Olancho: Allen 12529 (MO, TEFH); Santa Barbara: Allen 11696 (MO, TEFH). NICARAGUA. Matagalpa: Danin 4-J (MO). COSTA RICA. Alajuela: Crosby 10026 (MO); Cartago: Griffin 19477 (FLAS, PAC); Heredia: Grayum 9629 (MO); San Jose: Valerio 206 (FH, US). PANAMA. Bocas del Toro: Allen 5173 (MO); Chiriqui: Nee 14440 (MO); Darien: Concepcion 22 (PAC, PMA). World range: Southwestern U.S.A.; Mexico; Central America; Caribbean, Western, Northern, and Southern South America, Brazil.

Fissidens crispus is a common and extremely variable species, which can be recognized usually by the dark bronze color of the lower part of the stem and by the bistratose limbidium that ends below the leaf apex. The leaves are usually crispate when dry, nearly entire, and, except at the apices, limbate throughout. The limbidia on the dorsal and ventral laminae are typically 2 cells thick. The laminal cells are richly chlorophyllose, usually have bulging cell walls, and often appear to be arranged in discrete rows. The dorsal lamina, on the same plant, can end at the insertion or be decurrent for nearly an internodal length. The presence of axillary hyaline nodules distinguish this from related species.

9. *Fissidens curvatus*  

Plants with more or less dimorphic stems, the infertile stems to ca. 5 mm | ca. 1.5 mm, the fertile (perichaetial) stems 1.2-5 mm | 1-2 mm. Leaves with apex acuminate; margins more or less entire, limbate, the limbidia confluent; vaginant laminae acute, 1/2-2/3 the leaf length, more or less equal; costa percurrent to short excurrent; cells 8-14 um | 4-6 um, smooth, somewhat larger in the vaginant laminae; sporophyte terminal.

Illustrations. Koch (1951, Figs A-F, as *F. milobakeri*); Pursell (1960, Figs. 1-16, as *F. flavosetus*); Magill (1981, Fig. 11 1-8).

Habitat. On soil; ca. 2000 m.

Distribution in Central America. HONDURAS. Morazan: Allen 11259 (MO, TEPH).

World range: Southwestern U.S.A.; Mexico; Central America; Caribbean, Western, Northern and Southern South America, Brazil; Southern Africa; Australia, New Zealand.

*Fissidens curvatus* is a variable species that is distinguished by its small size and dimorphic stems. The leaves of the fertile stems are usually much larger than those on
the infertile stems. In leaves of both stems, however, the limbidium is usually prominent and confluent apically with the short-excurrent costa. Small, inconspicuous axillary hyaline nodules are also present.


Plants to ca. 8 mm | ca. 2 mm. Leaves 1 mm | 0.4 mm; apex acute to apiculate; margins crenulate-serrulate, limbate on the vaginant laminae of perichaetial and subperichaetial leaves; vaginant laminae more or less 1/2 the leaf length, more or less equal, acute; costa subpercurrent to percurrent; cells 6-10 um, unipapillose, papillae often forked, rounded to hexagonal. Sporophytes terminal; capsule more or less erect, cylindrical.

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11. Fissidens diplodus var. wainioi 12. Fissidens dissitifolius

Illustrations. Richards (1934, Fig. 1, as M. richardsii).
Habitat. Corticolous; 350-2500 m.
Distribution in Central America. BELIZE. Cayo: Allen 15074 (MO); Toledo: Allen 15361 (MO). PANAMA. Colon: Crosby 10453 (MO); Darien: Allen 8930 (MO, PAC).
World range: Mexico; Central America; Caribbean, Northern South America, Brazil.

Fissidens diplodus is a strictly corticolous species with a limbidium restricted to the vaginant laminae (1/2-1/3 its length) of the perichaetial and 1-2 subtending pair of leaves. The laminal cells are unipapillose. Other distinctive features include its numerous small perigonial branches, light green, cylindrical capsules, and short, erect, undivided to nearly undivided, sharply papillose peristome teeth.

Fissidens diplodus is presently the only Central American species reported with cylindrical capsules. However, there are two Colombian species (F. cylindraceus Mitt. and F. cylindrothecus Pursell & Aguirre) that have similar capsules. Fissidens cylindraceus differs in having pluripapillose leaf cells and peristome teeth divided to the base. In F. cylindrothecus the leaves are elimbate, the leaf cells are guttulate, and the peristome teeth are divided nearly to the base. In all three species the peristome teeth are erect when wet.

Moenkemeyera wainioi C. Mull. in Broth. var. mollis C. Mull., Hedwigia 39: 237. 1900. Type. Brazil, Ule 810 (H).

Distinguished from the typical variety by its low, unforked laminal papillae.
Illustrations. Grout (1943, Pl. 5 63-70, as F. muriculatus); Bartram (1949, Fig. 5
G-J, as F. muriculatus); Crum and Steere (1957, Fig. 5, as F. muriculatus).

Habitat. Corticolous at low elevations.
Distribution in Central America. BELIZE. Cayo: Allen 15513 (MO); Toledo: Allen 15346B (MO). GUATEMALA. Quezaltenango: Crosby 2840B (MO); Sacatepequez: Standley 88961a (FH). HONDURAS. Comayagua: Allen 11005 (MO, TEFH); Lempira: Allen 11337 (MO, TEFH); Yoro: Allen 13577 (MO). COSTA RICA. Alajuela: Brenes 11453a (NY); San Jose: Crosby 6374 (MO). PANAMA. Bocas del Toro: Allen 5811 (MO); Colon: Crosby 10476 (MO, PAC); Darien: Allen 8728 (MO); Panama: Salazar et al. 10544 (PAC, PMA); Veraguas: Crosby 102776 (MO).
World range: Mexico; Central America; Caribbean, Northern, Western and Southern South America, Brazil.

Cuba, Wright 14 (FH).

Plants to 14 mm | ca. 2.5 mm. Leaves to 2.8 mm | to ca. 0.3 mm; apex acute, sometimes obtuse and apiculate; margins entire, crenulate-serrulate at apex, limbate, limbidium 2-stratose; vaginant laminae more or less 1/2 the leaf length, more or less equal, acute; costa ending 3-16 cells below the apex; median cells (13-)18-27(-32) um | 9-14 um, larger and oblong in proximal parts of vaginant laminae, smooth, square to oblong to hexagonal. Sporophytes terminal.

Illustrations. Grout (1943, Pl. 1 8-10); Bartram (1949, Fig. 3 G-H).

Habitat. On soil along streams and in moist shaded areas at low to medium elevations.
World range: Mexico; Central America; Caribbean, Northern South America, Brazil.

Fissidens dissitifolius is closely related to F. reticulosus and F. mollis. Fissidens
mollis, however, has a 3-4-stratose limbidium that is confluent at the leaf apex, while the typically bistratose limbidium of F. dissitifolius and F. reticulosus ends short of the apex. In addition, Fissidens dissitifolius has smaller leaf cells (18-27 um | 9-14 um) than F. reticulosus (23-26 um | 13-18 um), and has erect symmetrical capsules and clusters of axillary, clavate, septate propagula.


   Plants to 2.5 cm | ca. 3.5 mm. Leaves to 3.5 mm | ca. 0.7 mm; apex obtuse to acute, often apiculate; margins crenulate-serrate at apices, elimbate; vaginant laminae more or less 2/3 the leaf length, unequal, minor laminae acute; costa percurrent to ending a few cells below apex; cells 7-10 um, irregularly bistratose, smooth but bulging, rounded-hexagonal. Sporophytes lateral.

   Illustrations. Grout (1936, Pl. 6); Jennings (1951, Pl. 15); Breen (1963, Pl. 1 5-6); Crum and Anderson (1981, Fig. 36 F-M); Ireland (1982, Pl. 49); Iwatsuki and Suzuki (1982, Figs. 6 2, 8 1-3; Pls. 46-47); Crum (1983, Fig. 17 C-E); Reese (1984, Fig. 15 G-J). All figures cited as F. cristatus.
   Habitat. Soil over tree bark; 1300 m.
   Distribution in Central America. GUATEMALA. Alta Verapaz: Richards et al. 2854 (PAC); HONDURAS. Comayagua: Standley 56201 (FH); COSTA RICA. Puntarenas: Crosby 3602 (MO).
   World range: Eastern Canada, North-Central, South-Central, Northeastern, Southeastern, and Southwestern U.S.A.; Mexico; Central America; Northern, Southwestern, Middle, East and Southeastern Europe; Caucasus, Western Asia, China, Soviet Far East, Eastern Asia; Indian Subcontinent, Malesia.

   Fissidens dubius, a widespread species in the Northern Hemisphere, reaches its southernmost New World distribution in Honduras. The species is distinguished by its
lighter colored, irregularly serrate leaf margins, irregularly bistratose laminal cells and

13. Fissidens dubius                14. Fissidens elegans

lateral sporophytes. Fissidens bourgaeanus also has irregularly bistratose laminal cells
and often irregularly serrate margins; however, it is a larger plant and the leaf margins
are usually darker in color.

Fissidens dubius is related to F. subbasilaris Hedw., which differs in having the
distal end of the costa obscured by chlorophyllose cells. Fissidens subbasilaris has not
been reported from Central America but is known from two states in Mexico.

    comm. Poiteau (B).
    Fissidens cuspidulatus Sull., Proc. Amer. Acad. Arts & Sci. 5: 274. 1861. Type. Cuba,
    Wright 16 (FH).

Plants to ca. 7.5 mm | ca. 1.5 mm. Leaves 0.8-1.6 mm | ca. 0.3 mm; apex acute, each ending in a clear, sharp cell; margins crenulate to serrulate, entire to remotely denticulate on vaginant laminae, limbate on vaginant laminae of perichaetial and/or sterile stems, variably limbate from the entire length to 3/4 or less the length of the vaginant laminae, limbidium unistratose; vaginant laminae more or less equal, 0.5-0.7 the leaf length; costa ending 5-8 cells below the apex to short-excurrent; cells (4-)5-7.5 um, pluripapillose, rounded-hexagonal. Sporophytes terminal.

Illustrations. Florschutz (1967, Pl. 1); Iwatsuki and Suzuki (1982, Pl. 2 14-27); Pursell (1984, Figs. 3, 26-27, as F. leptopodus; Figs. 11, 43-44).

Habitat. On rocks and boulders, especially limestone, and on soil; to 900 m.

Distribution in Central America. BELIZE. Cayo: Mains 4120 (FH, NY).
GUATEMALA. Alta Verapaz: Steyermark 44957 (FH); Peten: Bartlett 12155 (FH, MO, NY). HONDURAS. Comayagua: Allen 13682 (MO); Lempira: Allen 11151 (MO, TEFH); Olancho: Olson 83-8a (MO); Yoro: Allen 13515 (MO). COSTA RICA. Alajuela: Bowers 67-462 (PAC, TENN); Limon: Alfaro 110 (FH). PANAMA. Bocas del Toro: Allen 5526 (MO); Panama: Welch 20022 (NY, PAC).

World range: North-Central, South-Central, Northeastern, and Southeastern U.S.A.; Mexico; Central America; Caribbean, Western, Northern, and Southern South America, Brazil.

Fissidens elegans may be confused with F. intramarginatus, F. minutus, F. guianensis and F. neglectus. Fissidens intramarginatus differs in having a stronger limbidium that is consistently present on the vaginant laminae of all mature leaves and extends a short distance onto the adjacent part of the ventral lamina. The other three species differ in having either broadly acute and rounded or more or less obtuse leaves that do not end in a clear sharp cell. Fissidens weirii var. hemicraspedophyllus differs in having a limbidium two or more cell layers in thickness.

The limbidium of F. elegans can be on the vaginant laminae of most leaves of both perichaetial and sterile stems, restricted to the vaginant laminae of perichaetial and adjacent leaves or at times difficult to discern. In some populations the limbidium is
almost always marginal, while in others they are more or less intralaminal. In most populations the limbidium ends well below the distal ends of the vaginant laminae; occasionally, however, the limbidium closely approaches these distal ends. The costa in plants of the same populations and sometimes on the same plant can vary from ending a few cells below the leaf apex to being short-excurrent.

Skitophyllum fontanum B.-Pyl., J. Bot. (Desvaux), ser. 2, 4: 158. 1815. Type. Western France.
Fontinalis juliana Savi ex DC., Fl. Franc., ed. 3, 6: 236. 1815. Type. France, Duvan (G).
Octodiceras julianum (Savi ex DC.) Brid., Bryol. Univ. 2: 678. 1827.
Fissidens julianus (Savi ex DC.) Schimp., Flora 21: 171. 1838.
Schistophyllum julianum (Savi ex DC.) Lindb., Musci Scand. 13. 1879.

Plants to 12 cm long; leaves ca. 7 mm | ca. 0.6 mm; apex acute; margins more or less entire, elimbate; vaginant laminae 1/3(-1/2) the leaf length, unequal, minor laminae usually rounded; costa ending 15-25(-35) cells below the apex; cells 15-23 um | 10-18 um, smooth, mostly quadrate to oblong. Sporophytes terminal on short axillary branches.

Illustrations. Bartram (1949, Fig. 10 E-G, as F. debilis); Crum and Anderson (1981, Fig. 46 A-E); Pursell (1987, Figs. 1-14).
Habitat. Aquatic, on boulders in rivers; 10-1200 m.


World range: Western and Eastern Canada, Northwestern, North-Central, Northeastern, Southwestern, South-Central, and Southeastern U.S.A.; Mexico; Central America; Caribbean; Northern, Southwestern, Middle, East, and Southeastern Europe; Northeast Tropical Africa.

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15. Fissidens fontanus               16. Fissidens gardneri

Plants of Fissidens fontanus are delicate and feathery in appearance when submerged. Out of water the weak stems and flaccid leaves become very brittle upon
drying. The leaves are usually very long, to 7 mm, with an elimbate margin and a costa that ends 15-35 cells below the broadly acute apex. Vaginant laminae are usually less than 1/2 the leaf length, and usually the minor lamina is rounded and free distally. Sporophytes are unknown in Central American material, but the species typically has terminal perichaetia on short axillary branches and from 1 to 5 sporophytes per leaf axil. The seta and urn are more or less equal in length (0.5-0.6 mm long), and the peristome teeth are incompletely developed and often truncate.


Plants to 3.5 mm | 1.25 mm. Leaves 0.35-1.2 mm | ca. 0.2 mm; apex rounded; margins crenulate, weakly limbate on lower 1/2 of vaginant laminae of perichaetial leaves; vaginant laminae 2/3 the leaf length, unequal, minor laminae narrowed distally, ending on or near the costa; costa ending well below the apex, extending no more than 0.4-0.7 the distance between the vaginant laminae and the leaf apex; cells 6-7.5 μm, rounded hexagonal, pluripapillose. Sporophytes terminal.

Illustrations. Pursell (1984, Figs. 8, 45-48).
Habitat. Corticolous; low elevations, to 100 m.
Distribution in Central America. COSTA RICA. Guanacaste: Dodge & Thomas 6595 (FH).
World range: Mexico; Central America; Northern South America, Brazil.

Fissidens gardneri is one of the smallest pluripapillose species of section Semilimbidium C. Mull. Because of its small size it is easily overlooked. Although presently known in Central America only from Costa Rica, its distribution in this region is likely to be much broader.

In addition to its small size and pluripapillose laminal cells, the species can be recognized by its short costa that ends well below the obtuse leaf apex. Often the costa does not extend much beyond the vaginant laminae. A very weak limbidium is found on only the vaginant laminae of the perichaetial leaves. Moreover, the vaginant laminae
are unequal in length; the minor lamina is commonly narrowed distally and ends on or nearly on the costa.

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17. Fissidens goyazensis               18. Fissidens grandifrons  

Fissidens gardneri is closest to F. minutus, which differs in its larger size, nearly equal vaginant laminae, longer costa, and better developed limbidium found on the perichaetial leaves and 1-2 pairs of subtending leaves.


Plants to 5 mm | ca. 1.5 mm. Leaves 1.3 mm | to 0.4 mm; apex acute; margins entire, slightly crenulate near apex, limbate; vaginant laminae mostly equal, more or less 2/3 the leaf length; costa percurrent to excurrent; cells 5.5-7 um | 3.5-7 um, bluntly unipapillose, irregularly shaped. Sporophytes not seen.
Illustrations. Pursell (1966, Figs. 1-6, as F. veracruzensis).
Habitat. On moist soil; to 1350 m.
World range: Mexico; Central America; Caribbean, Brazil.

Fissidens goyazensis is closely allied to the highly variable F. crispus, but it is readily distinguished by its papillose leaf cells. Fissidens yucatanensis, another papillose species in section Fissidens, differs in its flaccid appearance, oblanceolate to ligulate leaves, larger (10-24 um) cells, flexuous costa, which is either percurrent or ends 4-5 cells below the apex, and the large, pellucid cells in the lower parts of the vaginant laminae. Fissidens angustifolius and F. panamensis differ also in having enlarged, pellucid cells in the vaginant laminae.


Plants to 10 cm | ca. 4 mm. Leaves ca. 3 mm | ca. 0.55 mm, pluristratose; apex rounded acute to obtuse; margins more or less entire, elimbate; vaginant laminae 1/2-2/3 the leaf length, more or less equal, acute; costa ending below the apex; cells 7-13 um, smooth. Sporophytes lateral from upper leaf axils.

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19. Fissidens guianensis

Illustrations. Bartram (1949, Fig. 10 C-D); Crum and Anderson (1981, Fig. 45 F-K); Iwatsuki and Suzuki (1982, Fig. 8 11-12, Pls. 53-54).

Habitat. Terrestrial or aquatic on rocks or gravelly soil in or along streams; 2400 m.

Distribution in Central America. GUATEMALA. Huehuetenango: Steyermark 50004 (FH, MO); Quiche: Sharp 5264 (NY); San Marcos: Steyermark 36897 (FH).

World range: Subarctic America, Western and Eastern Canada, Northwestern, North-Central, Northeastern, Southwestern, and Southeastern U.S.A.; Mexico; Central America; Southwestern and Middle Europe; Western Asia, Caucasus, Soviet Middle Asia, China, and Eastern Asia; Indian Subcontinent; Western Indian Ocean.

Fissidens grandifrons is distinguished by its long (to 4 cm) rigid stems and pluristratose leaves (unistratose at the margins). Characteristically the plants are dark brownish green and grow in dense mats in or along streams over limestone or in trickling waterfalls.


Plants 2.7-5.0 mm | ca. 2.0 mm. Leaves ca. 1.3 mm | ca. 0.3 mm; apex obtuse or abruptly short rounded; margins serrulate-crenulate, limbate on lower 1/2 or less of most vaginant laminae, limbidia unistratose; vaginant laminae unequal, acute, 1/2-2/3
the leaf length; costa ending 2-4 cells below the apex; cells (4-)5-6 um, rounded-
hexagonal, pluripapillose. Sporophytes terminal.

Illustrations. Florschutz (1964, Fig. 12a); Pursell (1984, Figs. 35-37).

Habitat. Primarily corticolous at low elevations.

Distribution in Central America. BELIZE. Toledo: White s.n. (FH, MO).
HONDURAS. Yoro: Allen 13539 (MO). COSTA RICA. Cocos Island [Puntarenas]:
Stewart 1349a (CAS); Alajuela: Crosby 9992 (MO). PANAMA. Bocas del Toro:
Salazar et al. 1769 (PAC, PMA); Canal Area: Steyermark 17492 (MO); Colon: Mori
& Kallunki 2835 (MO); Darien: Allen 8795 (MO); Panama: Crosby 10417 (MO).

World range: Central America; Caribbean, Western and Northern South America,
Brazil.

Fissidens guianensis has two varieties, guianensis and pacaas-novosensis Pursell &
Reese, separated principally on the extent of the limbidium. Only variety guianensis is
known from Central America.

Variety guianensis has obtuse to rounded (sometimes abruptly narrowed) leaf apices
and has been confused often with F. minutus, from which it differs in having a
limbidium on the lower half of the vaginant laminae of all well-developed leaves of
both sterile and fertile plants. At times, however, the limbidium is poorly developed
and found only near the leaf insertion. These are the forms confused with F. minutus.

Brazil, Martius s.n. (M).
Fissidens legalloi Crum, Bryologist 63: 97. 1960. Type. Guadeloupe, ile Saint-Barthelemy,
Le Gallo 674 (CANM).

Plants to ca. 7 mm | ca. 2 mm. Leaves to ca. 1.7 mm | ca. 0.5 mm; apex acute to
apiculate, usually ending in a sharp clear cell; margins serrulate, limbate along the
lower 2/3 or less of the vaginant laminae of most leaves; vaginant laminae 1/2-3/5 the
leaf length; costa ending 1-2 cells below apices to percurrent; cells 6-8 um,
unipapillose, quadrate to hexagonal. Sporophytes terminal.

Illustrations. Crum (1960, Figs. 9-12, as F. legalloi).

Habitat. On twigs; 1750 m.

Distribution in Central America. GUATEMALA. Baja Verapaz: Sharp 5163 (FH).
HONDURAS. Comayagua: Allen 10985, with F. papillosus (MO, TEFH); Lempira:
Fissidens hornschuchii is related to F. intermedius and F. sharpii. From the former it differs by its shorter limbidium that does not exceed and only occasionally reaches 3/4 the length of the vaginant laminae. Fissidens sharpii differs in having broad vaginant laminae that appear to encircle the stem.


Plants to ca. 2.5 mm | ca. 1.2 mm. Leaves ca. 1 mm | ca. 0.35 mm; apex acute; margins serrulate-crenulate, entire to slightly denticulate on the vaginant laminae, limbate along the entire length of the vaginant laminae; vaginant laminae ca. 1/2 the leaf length, acute; costa percurrent to ending 2-3 cells below the apex; cells 5-7 µm, unipapillose, quadrate to hexagonal. Sporophytes terminal.

Illustrations. Florschutz (1964, Fig. 14).
Habitat. On soil; sea level.
Distribution in Central America. PANAMA. Panama: Allen 4907 (MO).
World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil; North Central Pacific.

Fissidens intermedius is related to F. sharpii. Both usually have a percurrent costa. In F. sharpii, however, the vaginant laminae are very broad and nearly encircle the stem. In F. intermedius they are narrower and more typical of the type found in most species of Fissidens. Moreover, the limbidium on most leaves of F. intermedius usually extends the length of the vaginant laminae and may run onto the adjacent ventral lamina. In F. sharpii the limbidia on all leaves except the perichaetial ones typically end below the distal ends of the vaginant laminae. The leaf cells of F. intermedius are also smaller (5-7 µm long) than those of F. sharpii (7-12 µm long).
21. Fissidens intermedius  


Fissidens willisiae Bartr. in Willis, Bryologist 42: 152. 1939. Type. Panama, Willis 35 (FH).

Plants (3-5)-6-9(-14) mm | ca. 2 mm. Leaves (0.5-)-0.9-1.5(-1.7) mm | ca. 0.3 mm; apex acute; margins crenulate-serrulate, limbate on all vaginant laminae, limbidia unistratose, extending onto lower part of ventral laminae; vaginant laminae more or less 1/3 the leaf length, equal, acute; costa percurrent to short excurrent; cells (4-)-5-6(-7) \( \mu \)m, pluripapillose, rounded-hexagonal. Sporophytes terminal.

Illustrations. Steere (1936, Pl. 1, as F. hancockianus); Willis (1939, Fig. 1 a-d, as F. willisiae); Pursell (1984, Figs. 1-3).
Habitat. Along streams on soil and rocks at medium elevations.

Distribution in Central America. HONDURAS. Comayagua: Allen 13701 (MO); Lempira: Allen 11512 (MO, TEFH); Olancho: Allen 12569 (MO, TEFH); Yoro: Allen 13468 (MO). COSTA RICA. Cocos Island [Puntarenas]: Weber B-14329 (COLO, PAC); Heredia: Crosby 9896 (MO); San Jose: Svihla 2782 (FH). PANAMA. Canal Area: Willis 35 (FH); Cocle: Crosby 4407C (MO); Colon: Salazar et al. 4468 (PAC, PMA); Darien: Allen 9006 (MO, PAC); Panama: Willis 36 (MO); Veraguas: Crosby 10147 (MO).

World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

This species has been confused with Fissidens elegans. Fissidens intramarginatus, however, has a limbidium that extends the length of the vaginant laminae on all the leaves and onto the adjacent part of the ventral lamina. In contrast, the limbidium of F. elegans usually does not extend the full length of the vaginant laminae and is not always present on all the leaves.

Fissidens intramarginatus may also be confused with F. weirii var. hemcraspedophyllus, from which it differs by its unistratose limbidium and smaller leaves. In F. weirii var. hemcraspedophyllus the limbidium is 2-3-stratose.
23. Fissidens juruensis var. percurrens


Plants to 5 mm | 3 mm. Leaves ca. 2 mm | 0.4 mm; apex acute; margins crenulate-serrulate; vaginant laminae ca. 1/2 the leaf length, somewhat unequal at the insertion, acute; costa percurrent; cells 20-56 um | 13-22 um, smooth, thin-walled, median cells hexagonal, enlarged, oblong and pellucid in distal half of vaginant laminae. Sporophytes terminal.

Illustrations. None.
Habitat. On soil at low elevations.
Distribution in Central America. BELIZE. Cayo: Mains 3830 (DUKE, FH, MICH).

World range: Mexico; Central America.

This species was described by both Brotherus and Grout as elimbate, but there is a very weak, unistratose limbidium present on the lower parts of the vaginant laminae. The large, hexagonal leaf cells (20-56 um | 13-22 um) shrink when dry and are difficult to rehydrate.

There are two varieties, distinguished by costa length. In var. juruensis the costa ends 11-20 cells below the leaf apex while in var. percurrens it is percurrent.


Plants to ca. 1.45 cm | 3.0 mm. Leaves ca. 1 mm | 0.5-0.6 mm; apex rounded-obtuse to broadly acute; margins serrulate-crenulate, limbate on proximal 1/2 or less of
vaginant laminae of most leaves, limbidia unistratose; vaginant laminae acute, more or less 2/3 the leaf length; costa ending 2-4 cells below apex; cells 7-10 µm, smooth, guttulate, irregularly hexagonal. Sporophytes terminal.

Illustrations. Florschutz (1964, Fig. 13 A-G).

Habitat. On tree bark, roots and twigs at low elevations.

Distribution in Central America. HONDURAS. No locality: Wilson 48a (NY).
COSTA RICA. Limon: Steere CR-64 (NY).

World Range: Central America; Northern South America, Brazil.

Fissidens pellucidus, the Central American species most closely related to F. leptophyllus, differs in having elimbate leaves. Both species are guttulate, but the guttulae in F. leptophyllus are not as pronounced as those in F. pellucidus.

25. Fissidens minutus Thwait. & Mitt. in Mitt. var. minutus, J. Linn. Soc., Bot. 13:
Plants to 5 mm | 1.5 mm. Leaves (0.5-)0.7-1.0(-1.2) mm | 0.2-0.4 mm; apex broadly rounded-obtuse to acute; margins serrulate, limbate on lower 1/3-1/2 of vaginant laminae of perichaetial and 1-2 subtending pairs of leaves; vaginant laminae equal, acute, 1/2-2/3 the leaf length; costa ending 3-8(-16) cells below the apex; cells (4.5-)6-7(-8) um, pluripapillose, rounded-hexagonal. Sporophytes terminal.

Illustrations. Grout (1936, Pl. 7 A, as F. garberi); Crum and Anderson (1981, Fig. 39 A-E, as F. garberi); Pursell (1984, Figs. 5, 28-29).

Habitat. On soil, rocks and tree bark at low to moderate elevations.

Distribution in Central America. BELIZE. Toledo: Boutin & Schlosser 5156 (MO, PAC). GUATEMALA. Alta Verapaz: Steyermark 44968 (FH); Peten: Bartlett 12485 (MO).

World range: Southeastern and Southwestern U.S.A.; Mexico; Central America; Caribbean, Western and Northern South America, Brazil; China, Eastern Asia; Indian Subcontinent, Indo-China, Malesia.

Fissidens minutus var. minutus has a limbidium restricted to the lower 1/3-1/2 of the perichaetial and subtending leaves and a strong costa that usually ends 3-8 cells below the broadly rounded to acute leaf apex. The species may be confused with F. guianensis but in that species a limbidium may be found on all the leaves. However, the limbidium of F. guianensis is sometimes difficult to discern and may be present only in the lower 1/3 of the vaginant laminae.

Plants (0.9-1.2-2(-2.1) mm long. Leaves (0.4-0.5-0.6(-0.8) mm long; apex rounded to acute; margins serrulate, indistinctly limbate on lower 1/3-1/2 of vaginant laminae of the perichaetial and subtending leaves; vaginant laminae 1/2-2/3 the leaf length, more or less equal, acute; costa ending several cells below the apex; cells (4.5-6-7(-8) um, pluripapillose, rounded-hexagonal. Sporophytes terminal.

Illustrations. Steere (1937, Figs. 1-7, as F. pusillissimus); Bartram (1949, Fig. 6 C-D, as F. pusillissimus); Pursell (1984, Figs. 9-10, as F. microcladus var. pusillissimus).

Habitat. On tree bark.
Distribution in Central America. BELIZE. Belize: Gentle 1833a (FH, MICH).
World range: Mexico; Central America; Caribbean, Northern South America, Brazil.

This variety is smaller than var. minutus (stems 1.2-2.0 mm vs. 1.5-3.0 mm; leaves 0.5-0.6 mm vs. 0.7-1.0 mm), and its limbidium is less distinctly expressed. If the limbidium is not recognized, the species can be confused with F. gardneri. However, in F. gardneri the minor lamina either ends on or very near the costa, which does not extend much beyond the vaginant laminae. In the variety pusillissimus the minor lamina ends near the leaf margin and the costa is longer.


Plants to 15 mm | ca. 5 mm. Leaves to 5.5 mm | ca. 0.5 mm; apex acute to obtuse and apiculate; margins entire, often serrulate near the apex, limbate on all laminae, 3-4-stratose; vaginant laminae more or less equal, acute, ca. 1/5 the leaf length; costa percurrent to ending several cells below the apex; cells 18-49 um | 14-23 um,
smooth, quadrate to hexagonal; clusters of clavate, septate propagula commonly present in leaf axils. Sporophytes terminal.

Illustrations. Grout (1943, Pl. 1 14-22); Florschutz (1964, Fig. 5).

Habitat. On rocks and soil, often along streams and waterfalls at moderate elevations.

Distribution in Central America. BELIZE. Toledo: White s.n. (MO). GUATEMALA. Izabal: Steyermark 41781a (FH). HONDURAS. Olancho: Allen 12433 (MO, TEFH); Yoro: Allen 13617 (MO, TEFH). COSTA RICA. Cartago: Arrocha et al. CA674 (PAC); Guanacaste: Bowers 465-b (PAC, TENN); Puntarenas: Bowers 331-c (PAC, TENN); San Jose: Bowers 814 (PAC, TENN). PANAMA. Bocas del Toro: Allen 5815 (MO); Canal Area: Nee 6562 (MO); Chiriqui: Salazar et al. 601 (NY);

Colon: Crosby 10775 (MO, PAC); Darien: Allen 9002 (MO); Panama: Crosby 10422 (MO); Veraguas: Crosby 10237 (MO).

World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

Fissidens mollis is one of three Central American species (with F. dissitifolius and F. reticulosus) with limbidia on all leaf laminae and large, hexagonal, thin-walled, laminal cells. Fissidens juruensis var. percurrens has similar leaf cells, but its limbidium, restricted to the vaginant laminae, is only weakly differentiated.
27. Fissidens mollis  

In this species the limbidium is 3-4-stratose and confluent at the leaf apex. Moreover, the plants are typically to 15 mm long. Both F. dissitifolius and F. reticulosus are smaller plants with a bistratose limbidium that ends below the leaf apex. Clusters of clavate, septate propagula are usually present in the leaf axils of F. mollis.


Plants 6.5(-8.5) mm | ca. 2 mm. Leaves 1.0-1.3(-1.6) mm | 0.2-0.3 mm; apex gradually narrowed to rounded apices; margins serrulate, limbate intramarginally on lower 0.5-0.66 of vaginant laminae of perichaetial and most upper leaves; vaginant laminae more or less equal, acute, ca. 0.5-0.66 the leaf length; costa ending 2-6 cells below the apex; cells (4-)5-7 um, pluripapillose, rounded-hexagonal. Sporophytes terminal.

Illustrations. Crum (1960, Figs. 5-8); Pursell (1984, Figs. 6, 40).

Habitat. On soil and rocks at low to moderate elevations.

Distribution in Central America. BELIZE. Toledo: Allen 15477 (MO).
HONDURAS. Olancho: Allen 12795 (MO, TEFH). COSTA RICA. Cocos Island [Puntarenas]: Weber B-14329 (COLO, PAC). PANAMA. Bocas del Toro: Allen 5149 (MO); Canal Area: Willis 36 (FH); Panama: Crosby 4484 (MO); Darien: Allen 8758 (MO); Veraguas: Crosby 10205 p.p. (MO).

World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

Fissidens neglectus has an intralaminal limbidium confined to the lower 1/2 to 2/3
of the vaginant laminae of the perichaetial and uppermost leaves, and a costa that ends short of the leaf apex.


Plants to 2.5-9 mm | to 1.5-2.5 mm. Leaves 1-2 mm | ca. 0.2-0.4 mm; apex acute; margins more or less entire to serrate; vaginant laminae more or less 1/2 leaf length, minor laminae ending on costa or intermediate between costa and margin; costa short to long excurrent; cells 18-40 um long, marginal 2-3 rows 7-14 um long, smooth to more or less bulging, cells guttulate, oblong to hexagonal, irregularly so at margins. Sporophytes terminal.

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29. Fissidens ornatus                30. Fissidens panamensis

Illustrations. Herzog (1925, Fig. 6).

Habitat. On soil at low elevations.

Distribution in Central America. PANAMA. Colon: Crosby 10303 (MO, PAC); Panama: Salazar & Chung 7102 (PAC, PMA).

World range: Central America; Caribbean, Western and Northern South America, Brazil.

The laminal cells of two conspicuous sizes make Fissidens ornatus an easy species to recognize. The outer 2-3 rows are conspicuously smaller than those found in the
inner parts of the leaf. Moreover, the costa is typically long-excurrent and the cells are guttulate.


Plants to 2.5 mm to 1.5 mm. Leaves to 1.2 mm ca. 0.2-0.3 mm; apex apiculate; margins more or less entire, crenulate-denticulate at apices, limbate on all laminae, limbidia 1-2-stratose on dorsal and ventral laminae; vaginant laminae more or less equal, acute, 1/2-2/3 the leaf length; costa ending well below (as many as 2-4 cells) the apex; cells 10-14 um | 9-13 um, smooth, enlarged, oblong and pellucid in juxtacostal parts of vaginant laminae, otherwise strongly mammillose (unipapilloose), irregularly quadrate to hexagonal. Sporophytes unknown.

Habitat. On bare soil near sea level.
Distribution in Central America. PANAMA. Panama: Allen 4906 (MO, PAC, PMA).
World range: Central America.

Fissidens panamensis has leaves that are limbate on all laminae, unipapillate laminal cells and enlarged, pellucid juxtacostal cells in the vaginant laminae. These features also characterize F. angustifolius and F. yucatanensis. Fissidens panamensis, however, differs from F. angustifolius by having the costa typically ending several cells below the leaf apex and having short, crenulate marginal cells at the proximal ends of its dorsal laminae. Fissidens angustifolius, on the other hand, has a percurrent to short-excurrent costa and a limbidium that descends to the base (or nearly so) of the dorsal lamina. Fissidens yucatanensis is very close to F. panamensis, but it has larger laminal cells and a percurrent (or nearly so) costa.

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31. Fissidens papillosus

32. Fissidens pellucidus


Plants to ca. 3 mm | ca. 2 mm. Leaves to 1.6 mm | ca. 0.3 mm; apex obtuse to acute; margins serrulate-dentate, often coarsely so on vaginant laminae, elimate; vaginant laminae unequal, ca. 1/2 the leaf length; costa ending 2-4 cells below the apex; cells 7-11 um, mammillose (unipapillose), hexagonal. Sporophytes terminal.

Illustrations. Britton (1919, Pl. 233, as F. donnellii); Bartram (1949, Fig. 7 E-F, as F. donnellii); Iwatsuki and Suzuki (1982, Fig. 3 6, Pl. 28); Iwatsuki & Suzuki (1989, Fig. 7).

Habitat. On road banks; moderate elevations to 1500 m.
Distribution in Central America. GUATEMALA. Quezaltenango: Standley 84317 (FH). HONDURAS. Lempira: Allen 11375 (MO, TEFH). COSTA RICA. San Jose:
World range: Southeastern U.S.A.; Mexico; Central America; Caribbean, Western, Northern, and Southern South America, Brazil; China, Eastern Asia; Malesia; Macronesia, Middle Atlantic Ocean, Western Indian Ocean; Southwestern Pacific.

The leaves of Fissidens papillosus are mostly narrowly oblong, to 1.6 mm long, flabelliform in arrangement, and with the costa generally ending 2-4 cells below the obtuse to acute leaf apex. This species is close to F. steerei which has oblong-ovate leaves, lanceolate perichaetial leaves, and a costa that ends several cells below the obtuse to broadly acute apex. Furthermore, F. papillosus has a dentate leaf margin (coarsely dentate on the vaginant laminae), while that of F. steerei is crenulate.


   Plants to ca. 8 mm | ca. 2 mm. Leaves ca. 1.7 mm | ca. 0.3 mm; apex acute to bluntly acute; margins entire to crenulate-serrulate, elimbate; vaginant laminae unequal, more or less acute, to 1/2 the leaf length; costa ending 2-4 cells below the apex to short excurrent; cells 11-20 um, smooth to bulging, irregularly hexagonal. Sporophytes terminal.

   Illustrations. Bartram (1949, Fig. 6 A-B); Florschutz (1964, Fig. 16 B, as F. prionodes f. flexinervis, Fig. 16 C, as F. prionodes f. hornschuchii); Crum and Anderson (1981, Fig. 37 G-I).

   Habitat. On soil and tree bark; near sea level to 2000 m.
Distribution in Central America. BELIZE. Cayo: Allen 15111 (MO). GUATEMALA. Baja Verapaz: Sharp 5181 (FH, PAC, TENN). HONDURAS. Comayagua: Allen 12326 (MO, TEFH); Lempira: Allen 11306 (MO, TEFH); Olancho: Allen 12692 (MO, TEFH); Yoro: Allen 13474 (MO). COSTA RICA. Cocos Island (Puntarenas): Weber B-14304 (MO); Cartago: Arrocha CA889 (PAC); Puntarenas: Bowers 534-6 (PAC, TENN); San Jose: Skutch 2494 (FH, NY). PANAMA. Bocas del Toro: Allen 5087 (MO, PAC); Canal Area: Nee 6745 (MO); Chiriqui: Salazar et al. 637b (PAC, PMA); Cocle: Salazar et al. 1489 (NY); Colon: Salazar et al. 4194 (PAC, PMA); San Blas Comarca: Allen 4984B (MO); Darien: Allen 8993 (MO); Panama: Crosby 4361 (MO, NY).

World range: Southeastern United States; Mexico; Central America; Caribbean, Western and Northern South America, Brazil; Eastern Asia; Indo-China, Malesia; Australia.

Fissidens pellucidus is an extremely variable species with a costa that ends well below the leaf apex to short-excurrent. The plants are generally light green and red-tinged in the costa and stem. The smooth laminal cells contain guttulae that can be mistaken for papillae.


Plants 1.5-5 mm | ca. 2 mm. Leaves to ca. 3 mm | ca. 0.4 mm; apex acute to rounded; margins serrate, often coarsely so on the vaginant laminae, elimbate; vaginant laminae slightly unequal, acute, ca. 1/2 the leaf length; costa percurrent to ending 2-4 cells below the apex; cells 7.5-13 um, slightly bulging to smooth, irregularly hexagonal, lower juxtacostal cells of the vaginant laminae enlarged and pellucid. Sporophytes terminal.

Illustrations. Pursell (1986, Figs. 10-12, as F. tamaulipasensis).
Habitat. On fallen tree trunks; 2600 m.

Distribution in Central America. GUATEMALA. Quezaltenango: Standley 84317 (FH). COSTA RICA. Puntarenas: Fielder 143 (MO); Heredia: Griffin et al. D218 (FLAS, PAC).
World range: Mexico; Central America; Western South America, Brazil.
Fissidens platyphyllus is close to F. papillosus from which it differs by having smooth laminal cells and very conspicuously enlarged pellucid juxtacostal cells in the lower part of the vaginant laminae.

33. Fissidens platyphyllus 34. Fissidens plurisetus


Plants to ca. 9 mm | ca. 3 mm. Leaves ca. 2.5 mm | ca. 0.4 mm; apex acute; margins entire to irregularly serrulate, limbate on all laminae; vaginant laminae equal, acute, more or less 1/2 the leaf length; costa percurrent to short excurrent; cells 4-5 um, irregularly bistratose, uni- to pluripapillose, quadrate to irregularly hexagonal, obscure. Sporophytes terminal, 1-6 per perichaetium.

Illustrations. Willis (1939, Fig. 1 A-D).
Habitat. On tree bark and on rocks; sea level to 550 m.
Distribution in Central America. NICARAGUA. Zelaya: Seymour 3073B (MO).
PANAMA. Canal Area: Robbins 15 (FH); Panama: Mori & Kallunki 3357 (MO, PAC).

World range: Central America; Northern South America.

This species is close to Fissidens weirii var. weirii. It differs in having a limbidium confluent with the percurrent costa and multiple (1-6) sporophytes per perichaetium.


Plants to 8 cm | ca. 9 mm. Leaves ca. 6 mm | ca. 1.5 mm; apex obtuse to broadly acute, bluntly apiculate; margins entire, denticulate at apex, elimbate; vaginant laminae more or less equal, acute, ca. 1/2 the leaf length; costa percurrent or ending 2-4 cells below the apex; cells (10-)15-16(-20) um, larger along the costa, smaller at margins, smooth, irregularly hexagonal. Sporophytes terminal on short axillary branches.

Illustrations. Hedwig (1801, Pl. 27); Sullivant (1864, Pl. 27); Grout (1936, Pl. 11 A); Bartram (1949, Fig. 9 E-G, Fig. 10 A-B, as F. oerstedianus); Crum and Anderson (1965, Figs. 2, 4, 7-8, 11-12, 15, 17); Crum and Anderson (1981, Fig. 31 A-E).

Habitat. On moist shaded soil or rocks often along small streams at moderately high elevations.

Distribution in Central America. BELIZE. Cayo: Allen 15049 (MO); Toledo: Allen 15356 (MO). GUATEMALA. Alta Verapaz: Turckheim 7722 (BM, H, NY); Baja Verapaz: Richards et al. 2703 (MO, NY); Huehuetenango: Steyermark 49748 (NY); -----------------------------------
35. Fissidens polypodioides 36. Fissidens radicans

San Marcos: Steyermark 37261 (NY); Zacapa: Steyermark 43318 (NY). HONDURAS.
Comayagua: Allen 13763 (MO); Cortes: Allen 14070 (MO); Lempira: Allen 11469 (MO, TEFH); Morazan: Allen 12352 (MO, TEFH); Ocotepeque: Allen 14417 (MO);
Olancho: Allen 12863 (MO, TEFH); Santa Barbara: Allen 11645 (MO, TEFH).
NICARAGUA. Without locality, Oersted (H); Rivas: Stevens 6547 (MO). COSTA
RICA. Alajuela: Liesner & Judziewicz 14840 (MO); Cartago: Crosby 9786 (MO,
NICH, PAC); Heredia: Stevens 13951 (MO); Limon: Davidse & Herrera 29225 (MO);
Puntarenas: Davidse et al. 26095 (MO, NY); San Jose: Crosby 9822 (MO). PANAMA.
Bocas del Toro: Allen 5072 (MO); Chiriqui: Allen 5508 (MO); Cocle: Crosby 4409 (MO, NY); Darien: Mori & Gentry 4451 (MO); Veraguas: Correa et al. 4891 (PAC, PMA).

World range: Northeastern, Southeastern and South-Central U.S.A.; Mexico;
Central America; Caribbean, Western and Northern South America; Eastern Asia,
China; Indian Subcontinent, Indo-China, Malesia.

Fissidens polypodioides, the largest species of the genus in Central America, often
has stems 8 cm in length and leaves to 6 mm long. The species may be confused with
F. asplenioides, another large terrestrial species, but plants of that species are never
more than 4-5 cm in length. In addition the leaves of F. polypodioides are slightly
crispate when dry, and the laminal cells, although bulging slightly, are of uniform

thickness. In F. asplenioides the leaves are usually curled tightly inward from the tips
when dry, and the laminal cells are lenticularly thickened. Finally, in F. polypodioides the marginal cells of the vaginant laminae are not differentiated from the interior cells, while in F. asplenioides they are longer, narrower than the interior cells, and obliquely oriented. Both species have a costa that generally ends below the leaf apex; those of F. asplenioides, however, are usually shorter.


Plants to 7.5 mm | to 2.5 mm. Leaves to 1.5 mm | 0.2-0.35 mm; apex bluntly acute to obtuse; margins crenulate, elimbate; vaginant laminae more or less unequal, acute, ca. 1/2 the leaf length; costa ending 4-12 cells below the apex; cells 7-8 um, smooth, appearing bulging but convex-thickened, rounded-hexagonal. Sporophytes terminal, peristome reduced.

Illustrations. Bartram (1949, Fig. 7 G-I); Florschutz (1964, Fig. 18); Bruggeman-Nannenga and Pursell (1990, Figs. 11-22).

37. Fissidens reticulosus 38. Fissidens rigidulus

Habitat. Principally corticolous at low elevations.

Distribution in Central America. BELIZE. Belize: Robertson (NY). NICARAGUA. Zelaya: Stevens 8546 (MO). PANAMA. Bocas del Toro: Robbins 14 (FH); Canal Area: Croat 15416 (MO); Colon: Crosby 10391 (MO).
World range: Mexico; Central America; Caribbean, Northern South America, Brazil.

Fissidens radicans is the only species in Central America with leaves that are regularly caducous. Often many of the stems in a collection will be nearly naked. The leaves of F. radicans are broadly acute to rounded-obtuse with the dorsal laminae ending at or very near the insertion. The species is closely related to F. allenianus, which has complete peristome teeth, persistent leaves with an abruptly narrowed apex, and dorsal laminae ending conspicuously above the insertion.


Plants to 8 mm | ca. 2.5 mm. Leaves ca. 2.5 mm | ca. 0.3 mm; apex acute to somewhat obtuse and apiculate; margins more or less entire, limbate on all laminae, limbidia 2-stratose; vaginant laminae equal, acute, ca. 1/2 the leaf length; costa ending 8-15 cells below the apex; cells 16-48 μm | 7-20 μm, smooth, bulging, mostly oblong-hexagonal. Sporophytes terminal.

Illustrations. Grout (1943, Pl. 111-13).

Habitat. On soil and rocks along streams in forests at low elevations.


World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

Fissidens reticulosus has a limbidium on all leaf laminae and large, hexagonal laminal cells and is closely related to F. mollis and F. dissitifolius. Its bistratose limbidium ends below the apex (3-4-stratose and confluent at the apices in F. mollis). It
differs from F. dissitifolius by its slightly longer leaf cells (16-48 um vs. 23-26 um), suberect, asymmetric capsules, and lack of axillary propagula. Fissidens dissitifolius has leaf cells 18-27 um | 9-14 um, erect and symmetric capsules, and clusters of axillary, clavate propagula.


   Plants to 6.5 cm | to 5 mm. Leaves 1.8-4.6 mm | 0.4-1.0 mm; apex acute to broadly acute; margins more or less entire, limbate on all laminae, mostly 4-5 cells thick; vaginant laminae equal, acute, 1/2-2/3 the leaf length; costa percurrent or nearly so; cells 5-10 um, bulging to smooth, rounded-hexagonal, irregularly uni-, bi- or tristratose. Sporophytes terminal.

   Illustrations. Grout (1943, Pl.3, Fig. 35-40); Bartram (1949, Fig. 5, D-F as F. steyermarkii); Bruggeman-Nannenga (1978, Fig. 4).
   Habitat. On rocks and stones in running water, waterfalls, seepage areas, and on moist shaded soil at high elevations.
   Distribution in Central America. GUATEMALA. Quezaltenango: Steyermark 33889 (FH); San Marcos: Steyermark 36576 (FH); Suchitepequez: Steyermark 35310 (FH).
   World range: Mexico; Central America; Western and Southern South America, Brazil; Malesia; Australia, New Zealand; Southwestern Pacific; Subantarctic Islands.

   In Fissidens rigidulus the dorsal and ventral laminae are variably bistratose to tristratose, and the laminal cells are small (5-10 um long), obscure, and richly chlorophyllose. The pluristratose, cartilaginous limbidium often remains attached to the stem (along with the costa) after the other leaf cells have eroded away. The limbidium
at times is confluent at the leaf apex.

Fissidens rigidulus does not appear closely related to any other Central American species, although it may be confused with F. plurisetus, which has pluripapillose laminal cells (see also F. crispus).


Plants to 6 mm | ca. 3 mm. Leaves ca. 2.6 mm | ca. 0.4 mm; apex acute to sharply acute; margins entire; limbidia poorly defined; vaginant laminae unequal, acute, more or less 1/2 the leaf length; costa ending well below the apex; cells ca. 125 um | 20 um, smooth, fusiform, prosenchymatous. Sporophytes terminal.

Illustrations. Florschutz (1964, Fig. 4).

Habitat. On soil; 1200-1350 m.

Distribution in Central America. BELIZE. Cayo: Allen 15102 (MO); Toledo: Allen 15354 (MO). HONDURAS. Comayagua: Allen 13797 (MO); Olancho: Allen 12831 (MO, TEFH); PANAMA. Darien: Allen 8879 (MO, PAC).

World range: Mexico; Central America; Western and Northern South America, Brazil.

Fissidens scariosus is the only Central American species with large, fusiform laminal cells. The leaves have a lustrous sheen that is also found in F. pellucidus, but that species has more or less isodiametric laminal cells.
39. Fissidens scariosus


Plants to 5 mm | 1 mm. Leaves 0.8 mm | 0.3 mm; apex acute; margins entire and limbate on vaginant laminae for 1/3-3/4 the leaf laminae, crenulate-serrulate on ventral and dorsal laminae; vaginant laminae slightly unequal, acute, 2/3-3/4 the leaf length; costa percurrent to short-excurrent; cells 7-12 um, sharply unipapillose, quadrate to irregularly hexagonal. Sporophytes terminal.

Illustrations. Pursell (1986, Fig. 37).
Habitat. On soil; near sea level.
Distribution in Central America. PANAMA. Panama: Allen 4908 (MO, PAC).
World range: Mexico; Central America; Caribbean, Western South America, Brazil.

Fissidens sharpii has broadly triangular, acute stem leaves with widespread, recurved vaginant laminae that nearly encircle the stem. The limbidium is restricted to the lower 3/4 of the vaginant laminae except on perichaetial leaves, where it extends the entire length of the vaginant laminae. This species is closely related to F. intermedius, but that species has lanceolate stem leaves, vaginant laminae that do not encircle the stem, and a limbidium that extends the entire length of the vaginant laminae and often a short distance onto the adjoining ventral lamina.

Fissidens diplodus may be confused with these two species, but it has a limbidium restricted to the perichaetial and uppermost leaves, cylindric capsules, and undivided peristome teeth.

Plants to 7-8 mm | ca. 1 mm. Leaves 0.5–0.95 mm | ca. 0.25 mm; apex obtuse to broadly acute; margins crenulate, elimbate; vaginant laminae unequal, acute, 1/2–2/3 the leaf length; costa ending several cells below the apex; cells 8–11 um, mammillose, rarely bulging, hexagonal. Sporophytes unknown.

Illustrations. Grout (1943, Pl. 7 100-104); Bartram (1949, Fig. 8 A–C).

Habitat. On soil and rock usually along streams in woods at low to moderate elevations.

Distribution in Central America. BELIZE. Toledo: Robertson (NY, PAC).
Fissidens steerei is a small moss with elongated stems, obtuse leaves, a costa that ends several cells below the apex, crenulate leaf margins, and conspicuously mammillose (unipapillose) laminal cells. It is related to F. papillosus, which differs by its narrowly oblong, denticulate-margined leaves that are typically flabelliform in arrangement. Furthermore, sporophytes are unknown in F. steerei but are commonly produced in F. papillosus.


Plants to 3 mm | ca. 1.25 mm. Leaves ca. 1.5 mm | ca. 0.2 mm; apex acute; margins more or less crenulate, elimbate; vaginant laminae 1/3 the leaf length, narrowed to the costa; costa mostly long excurrent; cells 12-32 um | 7-18 um, marginal ones smaller, smooth, oblong, oblong-hexagonal to rhombic. Sporophytes terminal.

Illustrations. Pursell and Reese (1980, Figs. 1-8).
Habitat. On bare soil at low elevations.
Distribution in Central America. PANAMA. San Blas Comarca: Allen 4957 (MO, PAC).
World range: Central America; Northern South America, Brazil.

Fissidens subulatus grows as small, scattered plants among persistent protonemata. The long, excurrent costa gives the plants a decided Dicranella-like appearance. Leaves are few and the dorsal lamina is typically poorly developed. The smooth, quadrate to
oblong laminal cells are guttulate.

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43. Fissidens taxifolius 44. Fissidens wallisii


Plants to 11 mm | ca. 3.5 mm. Leaves ca. 2.7 mm | ca. 0.6 mm; apex obtuse to broadly acute, cuspidate; margins more or less evenly serrulate, elimbate; vaginant laminae unequal, acute, ca. 2/3 the leaf length; costa extending into the cuspidate tip; cells 8-11 ūm, larger along the costa, bulging above, conspicuously mammillose on vaginant laminae, irregularly hexagonal. Sporophytes basal on short axillary branches.

Illustrations. Bartram (1949, Fig. 6 E-G); Crum and Anderson (1981, Fig. 33); Iwatsuki and Suzuki (1982, Figs. 6 7, 8 9-10, Pl. 42).

Habitat. On soil or tree bark at high elevations.

World range: Subarctic America, Eastern Canada, North-Central, Northeastern, Southwestern, South-Central, and Southeastern U.S.A.; Mexico; Central America; Brazil, Southern South America; Northern, Southwestern, Middle, East, and Southeastern Europe; Western Asia, Caucasus, Siberia, Soviet Far East, China, Eastern Asia; Indian Subcontinent, Malesia; Macaronesia, Northern Africa, Western Indian Ocean; New Zealand; North Central Pacific.

This widespread Northern Hemisphere species is recognized by its evenly serrulate leaf margins, stout costa ending in the cuspidate leaf apex, conspicuously mammillose laminal cells (most evident on the vaginant laminae), and sporophytes originating from short basal branches. It can be confused with Fissidens bourgaeanus, which is a much larger plant and has 3-5 rows of thick-wall, marginal leaf cells that are usually noticeably darker than the inner laminal cells.

44. Fissidens wallisii C. Mull., Linnaea 38: 574. 1874. Type. Colombia, Wallis (BM).

Plants 5-17 mm | to 3 mm. Leaves to 1.7-3.1 mm | ca. 0.2-0.5 mm; apex acute; margins dentate, especially on the vaginant laminae, limbate on all lamina; vaginant laminae more or less equal, to 1/2 the leaf length; costa percurrent; cells 5-11 um long, smooth, bulging, irregularly quadrate to hexagonal. Sporophytes terminal.

Illustrations. None.
Habitat. Along streams on rocks and soil at moderate elevations.

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45. Fissidens weirii var. weirii 46. Fissidens weirii var. hemicraspedophyllus


World range: Mexico; Central America; Western and Northern South America, Brazil.

Fissidens wallisii is closely related to F. crispus but differs in its distinctive dentate leaf margin that is particularly well-developed on the vaginant laminae. The leaves of F. wallisii also tend to be somewhat larger than those found in many expressions of F. crispus.


Plants (3.0-)3.5-6.5(-10) mm | to 3 mm. Leaves (1.0-)1.2-1.8(-2.1) mm | to 0.4 mm; apex acute to short-acuminate; margins entire to serrulate, limbate on all laminae, 2-4-stratose, ending below the apex but variable, sometimes lacking or almost lacking on dorsal and ventral laminae of some leaves; vaginant laminae equal, acute, to 1/2 the leaf length; costa percurrent to short excurrent; cells (4-)5-7(-8) um, pluripapillose, irregularly quadrate to hexagonal. Sporophytes terminal.

Illustrations. Grout (1943, Pl. 3 41-46); Bartram (1949, Fig. 5 A-C); Florschutz (1964, Fig. 9); Pursell (1984, Figs. 2, 18-22).

Habitat. Mostly on trees, but also on soil; 125-2600 m.

Distribution in Central America. BELIZE. Cayo: Allen 15163 (MO); Toledo: Allen...
Fissidens weirii is the largest Central American species of section Semilimbidium C. Mull. The typical variety of the species has a limbidium 2-4-stratose on all leaf laminae. The only other Central American species with this feature is F. plurisetus. However, F. weirii differs from that species by its limbidium that ends short of the leaf apex and sporophytes typically produced singly per perichaetium (occasionally 2). In F. plurisetus the limbidium is confluent with the percurrent costa and sporophytes are multiple (1-6 per perichaetium).


This variety differs from var. weirii by having a limbidium restricted more or less to the vaginant laminae. Occasionally the limbidium extends a short distance onto the adjoining ventral lamina. It can also occur at the proximal end of the dorsal lamina.

Illustrations. Pursell (1984, Figs. 24-25).
Habitat. On soil; to 3200 m.

Distribution in Central America. BELIZE. Cayo: Allen 15228B (MO). EL SALVADOR. Santa Ana: Watson 0008 (MO). HONDURAS. Comayagua: Allen 13865 (MO); Cortes: Allen 14051 (MO); Lempira: Allen 11255 (MO, TEFH); Morazan: Allen 12375 (MO, TEFH); Ocotopeque: Allen 14436 (MO); Olancho: Allen 12877 (MO, TEFH). COSTA RICA. Alajuela: Bowers 391-f (PAC, TENN); Cartago: Crosby 6319 (MO); Heredia: Crosby 6527 (MO); San Jose: Crosby 6212 (MO). PANAMA. Bocas del Toro: Allen 5058 (MO); Chiriqui: Crosby 4047B (MO); Panama: Salazar Allen 6709 p.p. (PMA).

World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

The variety hemicraspedophyllum has been confused with F. elegans and F. intramarginatus, two species with a unistratose limbidium. It is most similar to F. intramarginatus in appearance; both have limbidia on nearly all leaves. Fissidens intramarginatus, however, is a smaller species.


The distinguishing feature of this variety is its intralaminal, bistratose limbidium on the dorsal and ventral laminae.

Illustrations. Pursell (1984, Fig. 23).
Habitat. On tree bark and twigs; 350-450 m.
World range: Central America; Caribbean.


Plants to 8 mm to 3 mm. Leaves 2 mm 0.45 mm; apex broadly acute to obtuse;
margins entire, crenulate on lower parts of dorsal laminae, limbate, limbidium not reaching the base of the dorsal laminae; vaginant laminae equal more or less 1/2 the leaf length; costa percurrent to ending 4-5 cells below the apex, quite narrow distally; cells (10-)12-18(-24) μm, irregularly polygonal to hexagonal, enlarged and oblong in the lower vaginant laminae, mammillose to papillose, smooth in the lower vaginant laminae. Sporophyte unknown.

Illustrations. Steere (1935, Figs. 1-6).
Habitat. On moist soil at low elevations.

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47. Fissidens weirii var. insertus 48. Fissidens yucatanensis

Fissidens yucatanensis differs from F. angustifolius by its broader, obtuse leaves and larger leaf cells. Fissidens goyazensis differs by its more rigid appearance, lanceolate to ligulate leaves, smaller (5.5-7 μm) cells, percurrent to excurrent costa and smaller, firm-walled cells in the lower parts of the vaginant laminae. Fissidens yucatanensis is closest to F. panamensis, from which it differs by its percurrent to subpercurrent costa. For further comments see discussions under F. angustifolius, F. goyazensis, and F. panamensis.
Plants to 5.5 mm | 3 mm. Leaves to 2.5 mm | to 0.5 mm; apex acute to irregularly acute and apiculate; margins more or less entire, limbate on all laminae; vaginant laminae equal, acute, 1/2 the leaf length; costa percurrent to short-excurrent; cells 10-13(-18) um, greatly enlarged, more or less pellucid, smooth to somewhat bulging, mostly irregularly hexagonal, more or less oblong in lower parts of vaginant laminae. Sporophytes terminal.

Illustrations. Grout (1936, Pl. 7 E, as F. kegelianus); Florschutz (1964, Fig. 10, as F. kegelianus); Crum and Anderson (1981, Fig. 41 A-D, as F. kegelianus); Iwatsuki and Suzuki (1982, Pl. 13).

Habitat. Rotted tree trunks; to 550 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: Sharp 2983 (FH).
HONDURAS. Atlantida: Standley 55299 (FH, NY); Comayagua: Allen 12927 (MO, TEFH); Olancho: Allen 12416 (MO, TEFH); Yoro: Allen 13608 p.p. (MO).
NICARAGUA. Chinandega: Standley 11509 (FH). COSTA RICA. Cartago: Svihla 2999 (FH); Heredia: Grayum 9629 (MO); Limon: Steere CR-165 (NY, PAC).
PANAMA. Bocas del Toro: Allen 5572 (MO); Canal Area: Allen 4905 (MO); Cocle: Gomez 7 (PAC, PMA); Colon: Nee 6574 (MO); Darien: Allen 9009 (MO); Panama: Mori & Kallunki 3358 (MO).

World range: Mexico; Central America; Caribbean, Western, Northern, and Southern South America, Brazil; China, Eastern Asia; Indian Subcontinent, Indo-China, Malesia; Northwestern, Southwestern, and South-Central Pacific.

Fissidens zollingeri is a widely distributed species in neotropical lowlands. Typically the plants are pale green and frondiform. The leaves are limbate on all laminae and have large, oblong, pellucid juxtacostal cells in the basal parts of the vaginant laminae. It is closely related to F. angustifolius but differs by its smooth laminal cells (unipapillate in F. angustifolius).

Excluded species

Fissidens prionodes Mont.
Reported from Costa Rica by Reed and Robinson (1971), but the specimen on which the report was made cannot be located for verification.

Fissidens longifolius Brid.
All reports of this species from Central America can be referred to F. crispus Mont.
Fissidens viridulus (Sw.) Wahl.
All reports of this species in Central America can be referred to F. crispus Mont.

BRUCHIACEAE

Trematodon Michx., Fl. Bor. Amer. 2: 289. 1803.

Plants small, gregarious or loosely tufted; stems erect, simple. Leaves ovate-lanceolate; costa single, strong; alar cells not differentiated. Setae long or short; capsules exserted, long rostrate, with a strongly differentiated, stomatose neck, operculate; peristome present or absent. Calyptrae cucullate. Spores large, highly ornamented.

Trematodon is best recognized by its long-necked capsules. The genus has undifferentiated alar cells, an autoicious condition (in Central American species), vertically striate outer peristome surface, and subreniform spores. Collections without sporophytes cannot be distinguished from Dicranella or Ditrichum. Trematodon longicollis capsules are twisted at the neck when dry and on hydration move in circles much like those in Campylopus, where the motion is caused by its cygneous setae.

The Bruchiaceae consists of four genera, Bruchia, Eobruchia, Pringleella, and Trematodon, all of which have capsules with long, well-developed, stomatose necks and large, highly ornamented spores (see Buck 1979a). Trematodon differs from the others in having cucullate rather than mitrate calyptrae. Bruchia is the only cleistocarpous genus in the family.

Bruchia queenslandica Stone and Pringleella pleuridioides Card. occur in Mexico and so may be encountered in Central America. They differ from Trematodon in having mitrate calyptrae and immersed to emergent capsules. In addition, B. queenslandica has apiculate capsules, while P. pleuridioides is eperistomate.

1. Capsule neck equal to or shorter than urn; leaves abruptly narrowed above; margins erect; costa completely filling the awn
   1. T. ambiguous
1. Capsule neck twice as long as urn; leaves gradually narrowed above; margins weakly recurved; costa not occupying the width of the subula

2. T. longicollis


Plants scattered, yellowish green, terricolous; stems 3-10 mm long. Leaves evenly spaced, flexuous-spread when wet, 2-3 mm long, oblong and clasping at base; apex abruptly contracted to a long awn; margins erect, entire; costa percurrent, smooth, ventral surface abruptly expanding at base of awn and filling the upper leaf; upper cells quadrate to shortly rectangular, thick-walled, basal cells narrowly long-rectangular to rhomboidal, whitish yellow, thin-walls. Autoicous. Setae 7-16 mm long, yellow; capsules inclined, yellow or red, urns ellipsoidal, 1.0-2.0 mm long, neck 1.2-1.5 mm long, as long as or a little shorter than the urn; annuli deciduous, revoluble; opercula rostrate, 1.0 mm long; stomata phaneropore; peristome teeth red, lanceolate, vertically striate. Calyptrae yellow, 1.5 mm long. Spores papillose.

Illustrations. Grout (1936, Pl. 26 B); Takaki (1962, Fig. 4); Crum and Anderson (1981, Fig. 67 A-G); Ireland (1982, Pl. 69); Cao and Gao (1988, Fig. 6).
Habitat. On soil; 600-900 m.
Distribution in Central America. HONDURAS. Morazan: Standley 3973 (F).
NICARAGUA. Managua: Garnier (US).

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2. Trematodon longicollis

World range: Eastern and Western Canada, North-Central and Northeastern U.S.A.; Central America; Northern, Middle, Southwestern, and East Europe; Caucasus, China, Eastern Asia, Siberia, Soviet Far East; Indian Subcontinent.

A northern species reaching its southern limit in Central America, Trematodon ambiguus is separated from Trematodon longicollis by its shorter capsule neck, erect and entire leaf margins, and broader costa that flares outward at the base of the awn and nearly fills it.


Plants scattered, yellow-green, terricolous, 3-5 mm long. Leaves evenly spaced, flexuous spreading when wet, clasping, oblong to oblong-ovate at base, gradually long linear-subulate above, 2-3 mm long; margins weakly recurved above, entire below, weakly denticulate by blunt teeth above; costa percurrent; upper cells short-rectangular, walls firm and thickened; basal cells laxly oblong-rhomboideal to long rectangular, pale whitish yellow. Autoicous. Setae 10-15 mm long, smooth, yellow; capsules inclined, yellow, urn ellipsoidal 1.5-2.0 mm long, neck 3.0-4.0 mm long; annuli deciduous, revoluble; opercula rostrate, 1.0 mm long; stomata cryptopor and phaneropor stomata; peristome teeth red, lanceolate, vertically striate. Spores densely papillose or minutely warty.

Illustrations. Grout (1936, Pl. 25); Bartram (1949, Fig. 14 I-K); Takaki (1962, Fig.
Habitat. On soil; 20-1500 m.


World range: Eastern Canada, North-Central, Northeastern, and Southeastern U.S.A.; Mexico; Central America; Caribbean, Western South America, Brazil; Southeastern Europe; China, Japan; Indian Subcontinent, Indo-China, Malesia; Southern Africa; New Zealand; Northwestern, North-Central, Southwestern, and South-Central Pacific.

This species is marked by its longer-necked capsules and gradually narrowed leaves that have narrowly recurved, weakly denticulate margins. Trematodon ambiguus has abruptly narrowed leaves with erect margins that are obscurely roughened to entire and a costa that flares outward at the base of the awn to occupy the entire subula. Britton (1913) and Crum and Steere (1957) considered T. longicollis and T. reflexus C. Mull. synonymous; in Central America all collections named T. reflexus are identical to T. longicollis.
Plants minute to robust, closely tufted; stems erect (rarely pendent), simple, forked or irregularly branched. Leaves evenly distributed around the stem, mostly long-lanceolate, erect or secund, often crispate; costa single, ending near apex to excurrent; cells smooth or papillose; alar cells strongly differentiated or undifferentiated. Setae mostly elongate, straight, flexuous or cygneous; capsules erect or curved, cylindrical or ovoid, smooth or furrowed; annuli present and complex to simple or absent; stomata present or absent; peristome usually present, of 16 divided or entire teeth, striate or smooth below, papillose or smooth above. Calyptrae cucullate, entire or fringed at base.

The Dicranaceae are a large family difficult to characterize because of internal variability and intergradations with nearby families. In general the plants are erect, the leaves narrow, the costa single and well-developed, the setae elongate, the capsules exserted, and the peristome teeth have a 2:3 haplolepideous pattern. Crum and Anderson (1981) noted that well-developed alar cells are generally associated with the family, but undifferentiated alar cells are commonly encountered, and both character states are found in some genera.

In Central America the genera can be clustered into four, weakly demarcated subfamilies. The Paraleucobryoidae are here synonymized with the Campylopodioideae. This decision is necessitated by the close gametophytic relationship of Paraleucobryum and Campylopus. Sporophytically only the well-developed annulus of the Paraleucobryoidae separates the two. This character is of uncertain value in the Dicranaceae, due to its variable expression in the Anisothecioideae and the Dicranoideae.

The subfamilies and their genera, arranged systematically, are:

- Campylopodioideae: Campylopodiella, Campylopus, Bryohumbertia, Dicranodontium, and Pilopogon.
- Dicranoideae: Chorisodontium, Dicranum, Symblepharis, Holomitrium, Eucamptodontopsis, Schliephackea, Leucoloma, and Cynodontium.
- Rhabdoweisioideae: Rhabdoweisia.

Key to the Genera

1. Costa broad, 1/3 or more the leaf base width
   2
1. Costa narrow, less than 1/3 the leaf base width
2. Costa in cross section with a single ventral layer of enlarged hyaline cells

3. Costa in cross section with one or more layers of ventral stereid cells

4. Costa abruptly widened outward to nearly the leaf margins at midleaf
   10. Chorisodontium

5. Upper leaf cells linear
   8. Dicranodontium

6. Plants small, 0.5-2.5 cm high; leaves ovate-lanceolate, sheathing at base, abruptly contracted to the apex; spores warty
   4. Microcampylopus

7. Setae cygneous
   6. Campylopus
7. Setae straight or somewhat twisted to wavy

8. Stems evenly foliate; leaves erect appressed; perichaetial leaves sheathing, the apices nearly reaching the capsule

9. Pilopogon

8. Stems interruptedly foliate (with comal tufts); leaves spreading; perichaetial leaves not sheathing

7. Bryohumbertia

9. Alar cells clearly differentiated

10. Leaves with a hyaline border; upper cells pluripapillose

16. Leucoloma

10. Leaves without a hyaline border; cells smooth

11. Costa abruptly widened outward to nearly the leaf margins at midleaf

10. Chorisodontium

11. Costa gradually narrowed to the apex

12. Perichaetial leaves not sheathing; peristome teeth divided 1/2 the way to the base; capsules curved or erect

11. Dicranum

12. Perichaetial leaves long sheathing; peristome teeth not divided; capsules erect

13. Plants pendent; leaves spreading from base
15. Schliephackea
13. Plants in erect tufts; leaves erect at base
14
14. Leaves crispate 13. Holomitrium
15. Costa in cross section with a ventral and dorsal layer of hyalocyst cells, clusters of median stereid cells and a small group of ventral sub-stereid cells
5. Campylopodiella
15. Costa in cross section with dorsal stereid cells and median guide cells
16
16. Stems slenderly julaceous with leaves tightly appressed throughout 1. Aongstroemia
16. Stems with leaves crispate, flexuous, spreading or appressed at base and spreading above
17
17. Leaves crispate when dry 18
17. Leaves erect-spreading to flexuous when dry 21
18. Cells unipapillose; setae cygneous 17. Cynodontium
18. Cells smooth; setae straight
19
19. Plants small, 0.2-0.3 cm high; leaves spreading from insertion; capsules eight-ribbed when dry 18. Rhabdoweisia
19. Plants large, (0.5-)2-8 cm high; leaves clasping at base; capsules smooth
20. Perichaetial leaves long sheathing, the apices nearly reaching the capsule base; peristome entire

13. Holomitrium

20. Perichaetial leaves not sheathing; peristome teeth divided

12. Symblepharis

21. Capsule neck elongate, longer than the urn

Trematodon (Bruchiaceae)

21. Capsule neck inconspicuous, shorter than the urn

22

22. Annulus simple and persistent; stomata present; peristome attached above the capsule mouth on a short, smooth basal membrane

2. Anisothecium

22. Annulus compound and revolvable; stomata absent; peristome inserted at or below capsule mouth

23

23. Setae straight or flexuous

3. Dicranella

23. Setae cygneous

4. Microcampylopus

Anisothecioideae


Plants slender to elongate, terricolous; stems julaceous. Leaves appressed, oval to oblong; costa single, strong; cells elongate or oval, firm-walled and smooth; alar cells undifferentiated. Dioicus. Setae smooth, erect; capsules erect, ovoid-cylindrical; opercula rostrate; peristome teeth divided above or absent. Calyptrae cucullate.

Aongstroemia exhibits notable peristome variation, but its members are held
together by their julaceous stems with tightly appressed leaves. Although eperistomate species resemble Astomiopsis or Bryomanginia (Ditrichaceae), the peristomate species clearly belong in the Dicranaceae.

1. Costa long-excurrent; plants 4-6 cm high; upper leaf cells linear-vermiculose; leaf margins entire
   1. A. filiformis

1. Costae percurrent or ending below the apex; plants less than 1 cm high; upper leaf cells oval; leaf margins erose-denticulate

2. Leaves erect-appressed throughout; costa ending below the apex; leaf margins frequently erose-denticulate by double projecting cells
   2. A. julacea

2. Leaves secund at tips, erect-appressed below; costa percurrent or ending below the apex; leaf margins erose-denticulate by single projecting cells
   3. A. orientalis


Plants small to medium sized, laxly tufted to gregarious, yellow-green; stems 3-7 cm long, simple or irregularly branched. Leaves oblong-ovate, 4-5 mm long, clasping below, subulate above with a long or short awn, variously decurrent; margins plane, entire; costa filling the subula, long excurrent, smooth; upper cells linear-vermicular; basal cells shortly rectangular. Setae single or multiple, 3-4 mm long, yellow becoming red with age; capsules 1.5 mm long, red; annuli differentiated; stomata phaneropore;
peristome teeth lanceolate, red, papillose throughout, divided above into two or three prongs; opercula 1.0 mm long.

Illustrations. Bartram (1949, Fig. 15 A-C); Magill (1981, Fig. 31 1-9).

Habitat. On soil; 1380-3450 m.

Distribution in Central America. GUATEMALA. Quezaltenango: Sharp 2295 (FH, MO, NY, US); San Marcos: Steyermark 36442 (F, FH); Totonicapan: Standley 65920 (F, FH). COSTA RICA. Alajuela: Crosby & Crosby 6302 (MO); Cartago: Crosby 9788 (MO); Heredia: Crosby 9941 (MO). PANAMA. Chiriqui: Croat 10453 (MO, NY).

World range: Mexico; Central America; Caribbean, Western South America; Southern Africa, Western Indian Ocean.

Pilopogon and some species of Dicranodontium are macroscopically similar, but these taxa have well-developed alar cells, leaves less tightly appressed, longer setae (15 mm vs. 3-4 mm), and broader costa (1/3 the leaf width). In the neotropics this species has generally been known as Aongstroemia jamaicensis.

Gymnostomum julaceum Hook., Musci Exot. 1:42. 1818. Type. Ecuador, Humboldt & Bonpland.

Plants minute, delicate, scattered to gregarious, green to yellowish green; stems slender, 2-3(-10) mm long, irregularly and simply branched. Leaves minute, shortly-oval, 0.4-0.8 mm long; apex rounded-apiculate to obtuse; margins plane to weakly erect, erose-denticulate (frequently by double projecting cells in the upper two-thirds); costa ending below apex, smooth; upper cells oval-rhomboidal, incrassate, basal cells
2. Aongstroemia julacea 3. Aongstroemia orientalis

larger, quadrate to shortly rectangular. Sporophytes not seen from Central America, reported by Mitten (1869) as setae elongate, capsule oblong, annuli large, peristome absent.

Illustrations. Hooker (1818, Pl. 43); Gangulee (1971, Fig. 110); Magill (1981, Fig. 31 10-19).
Habitat. On soil; 3400-3500 m.
Distribution in Central America. COSTA RICA. Cartago: Holm & Iltis 1074 (FH).
World range: Mexico; Central America; Western South America; Siberia, Mongolia, China, Eastern Asia; Indian Subcontinent; Southern Africa, Western Indian Ocean.

This species is very close to Aongstroemia orientalis Mitt., which has less obtuse leaves that are appressed below but secund at the tips. In addition, the less stout costa frequently extends to the apex, and the leaf margins lack doubly projecting cells.

Syntypes. Bhutan, Griffith; Sikkim, Hooker & Bell; Burma, Kurz.
Plants minute, delicate, scattered to gregarious, yellowish; stems slender, erect to
arcuate, 2-10 mm long, simple or with a few branches. Leaves minute, ovate, appressed below and homomallous with secund points above, 0.5-0.8 mm long; apex broadly acute to obtuse; margins weakly incurved, erose-denticulate by projecting cells in the upper half; costa percurrent or ending just below the apex, smooth; upper cells oval-rhomboideal, incrassate, marginal cells obliquely long rhomboideal; basal cells quadrate to short rectangular, incrassate. Setae 8-10 mm long; capsules erect; peristome absent.

Illustrations. Bartram (1939, Pl. 2 28); Bartram (1949, Fig. 15 D-E); Gangulee (1971, Fig. 109); Li (1985, Fig. 9 1-9); Noguchi (1987, Fig. 54 A).

Habitat. On soil; 2400-4400 m.

World range: Mexico; Central America; Western South America, Brazil; Siberia, China, Eastern Asia; Indian Subcontinent; Indo-China, Malesia.

Exceedingly close to Aongstroemia julacea, both A. orientalis and A. julacea have erose-denticulate leaf margins, eperistomate capsules and are similar in size, leaf shape, and cell aerolation. In A. orientalis the leaves are usually secund at the tips, while in A. julacea they are smoothly julaceous to imbricate throughout. Aongstroemia orientalis sometimes has non-secund leaf tips, but its percurrent, less stout costa and lack of doubly projecting marginal leaf cells aid in its recognition. Gangulee (1971) reported A. orientalis from 19,800 ft. on Mount Everest, "probably the highest record for any moss."


Plants small, terrestrial, in tufts or mats; stems erect, simple or sparsely branched, radiculose at base. Leaves distant below and smaller than upper leaves, erect-spreading to recurved from an ovate-lanceolate or strongly clasping-ovate base, narrowly
lanceolate; margins entire below, serrulate above; costa single, stout, percurrent or excurrent; cells smooth; alar cells not differentiated. Dioicus. Setae elongate, erect and weakly flexuous to straight; capsules ovoid to oblong; annuli of several rows of small, thick-walled, non-revoluble cells; stomata present; opercula short rostrate; peristome teeth 16, well-developed, papillose to papillose-striate, divided, inserted above the mouth on a short, smooth basal membrane. Calyptrae cucullate, smooth.

Anisothecium belongs to a generic complex based entirely on sporophytic or sporophyte-associated characters - stoma, annulus, seta, spore - whose states are present in reticulate combinations. The value of individual characters within the complex is difficult to assess, since character states can be consistent and diagnostic in one element but variable in another. Many species cannot be placed when sporophytes are absent, and the complex is exclusively dioicus.

Anisothecium has been synonymized with Dicranella, but it is probably the complex member most worthy of generic recognition. The genus is marked by three features: 1. operculum shed by means of an annulus that consists of several rows of small, thick-walled, non-revoluble cells, 2. peristome teeth borne on a short, smooth basal membrane, and 3. stomata present. Within the complex the first two features uniquely define Anisothecium. The last feature is also found in Microcampylopus, but that genus has cygneous setae. Thus, Anisothecium differs from each member of the complex by three character states.

1. Leaves erect and sheathing at base; apex abruptly spreading to squarrose and setaceous; setae 10-12 mm long; capsules oblong, 1.5 mm long
   2. A. vaginatum

1. Leaves spreading from base, gradually narrowed, linear above; setae 4-7 mm long; capsules ovoid, to 1.2 mm long

2. Leaf margins plane, sinuate-dentate above, the outermost row of cells bulging, somewhat inflated; peristome teeth vertically striate-papillose on outer surface
   1. A. rufescens

2
2. Leaf margins recurved, entire except at the tips, outermost row of cells firm-walled; peristome teeth papillose on outer surface

3. A. varium


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<td>1. Anisothecium rufescens</td>
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Plants reddish brown; stems 5-10(-15) mm high. Leaves 1-2 mm long, lower leaves distant and spreading, upper leaves erect-spreading to subsecund, lanceolate-triangular, gradually narrowed to a broadly acute apex, somewhat keeled above; margins plane, slightly serrulate to sinuate-dentate above the leaf shoulders, serrulate at apex; costa broad, subpercurrent to shortly excurrent; leaf cells long rectangular, thin-walled, 6-10 um | 40-60 um long, marginal leaf cells somewhat inflated and bulging. Setae 5-7 mm long, red-brown, smooth; capsules 0.75 mm long, ovoid, reddish
brown, erect, symmetrical, smooth; opercula 0.5-0.6 mm long, conic at base, short-rostrate; peristome teeth 300-350 um high, red, striate-papillose, divided 1/2 their lengths, basal membrane 50 um high, smooth, darker red, with thicker trabeculae. Spores 16-25 um, lightly papillose, yellowish.

Illustrations. Husnot (1884, Pl. 7); Grout (1904, Pl. 12); Jennings (1951, Pl. 60); Nyholm (1954, Fig. 15 G); Smith (1978, Fig. 61 1-4); Crum and Anderson (1981, Fig. 71 G-K); Ireland (1982, Pl. 74); Nyholm (1986, Fig. 18 G); Frahm and Frey (1987a, Fig. 50 19).

Habitat. On soil of wet cliff and corticolous; 2000-2450 m.


World range: Northwestern and Eastern U.S.A.; Central America; Northern, Middle, and Eastern Europe; Caucasus, Siberia, Soviet Far East; Japan.

Anisothecium rufescens has triangular-lanceolate leaves gradually narrowed to an acute apex, a percurrent costa, and long-rectangular, thin-walled cells that are inflated and bulging at the margin. Its lowermost leaves are commonly reduced, and the perichaetial leaves are broadly ovate, frequently sheathing at the base of the setae. Anisothecium varium, with similar shaped leaves, has entire, narrowly, recurved leaf margins with firm-walled, non-bulging marginal leaf cells and evenly papillose peristome teeth. Dicranella harrisii, another species with bulging to inflated marginal leaf cells, has ovate-lanceolate leaves.

Plants large for the genus, gregarious or in loose tufts, dull green to yellowish; stems slender, 15-30(-40) mm high, with a julaceous appearance due to strongly clasping leaf bases. Leaves 3-4 mm long, obovate, strongly clasping at base, abruptly narrowed above to a widely spreading to squarrose, setaceous limb about the same length as the basal part of the leaf; margins entire below, slightly serrulate at the apex; costa percurrent and nearly filling the upper limb; lower leaf cells pale, rectangular, thin-walled, those at the shoulder smaller, subquadrate to transversely elongated, incrassate. Perichaetial leaves identical to vegetative leaves except the clasping base somewhat longer. Setae 10-12 mm long, erect, weakly flexuous to straight, red; capsules 1.5 mm long, erect, oblong; stomata in 1 or 2 rows at base of capsule; opercula 1.5-1.7 mm long, long subulate-rostrate; peristome teeth 16, reddish brown below, hyaline above, densely papillose, from a low, smooth, thickly trabeculate basal membrane, deeply divided into terete forks, 250 um long. Calyptrae smooth, entire at base, 2.0 mm long. Spores roughened, 20 um wide.

Illustrations. Hooker (1820, Pl. 141); Bartram (1949, Fig. 15 G-I).

Habitat. On moist shaded banks; 2280-2835 m.


COSTA RICA. Cartago: Crosby & Crosby 6170 (MO).

World range: Mexico; Central America; Caribbean, Western South America, Brazil.

The strongly clasping leaf bases give the stems a smoothly julaceous look. Also distinctive are the strong contrast between the elongate basal cells and its subquadrate to transversely elongate median leaf cells, and the costa that nearly fills the upper leaf. Some Dicranella species have clasping leaf bases (D. standleyi, D. longirostris, and D. brachyblepharis), but their leaves are never as strongly clasping throughout as found here.

This species has been treated in Anisothecium (Mitten 1869), Aongstroemia (Williams 1913), and Dicranella (Bartram 1949). Aongstroemia is similar in its clasping leaves, julaceous stems, elongate, stomatose capsules, and annulus-type. Anisothecium vaginatum differs in its spreading to squarrose upper leaf limb (erect, appressed...
throughout in Aongstroemia). The species is placed in Anisothecium because of the short basal membrane of its peristome.

Symplepharis and Holomitrium also have clasping leaf bases. But they are larger plants with crissate leaves and entire peristome teeth. Holomitrium also has differentiated alar cells.


Plants small in dull, dirty green to light green tufts; stems 3-10 mm high. Leaves 1-2 mm long, lanceolate-triangular from a lanceolate base gradually narrowed to a broadly acute apex, lower leaves distant and spreading, upper leaves erect spreading to sub-secund; margins irregularly recurved above, entire below, denticulate at the extreme tip; costa percurrent; cells oblong-linear, firm-walled throughout. Setae 5-7 mm long, red, erect to weakly flexuous; capsules 0.8-1.2 mm long, ovoid, erect to weakly inclined and curved, smooth, not strumose; opercula 0.5-0.7 mm long; peristome teeth 350-400 um long, red, lightly and evenly papillose, divided 1/2 their lengths, basal membrane 50 um, smooth, darker red, with thicker trabeculae. Spores 17-20 um, lightly papillose, yellowish.

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3. Anisothecium varium

Illustrations. Husnot (1884, Pl. 7); Grout (1904, Pl. 13); Bartram (1949, Fig. 16 D-F); Jennings (1951, Pl. 11); Nyholm (1954, Fig. 18 E); Welch (1957, Fig. 52); Breen (1963, Pl. 19 5-7); Lawton (1971, Pl. 27 7-14); Smith (1978, Fig. 59 7-11); Crum and Anderson (1981, Fig. 71 A-F); Ireland (1982, Pl. 73); Crum (1983, Fig. 27 C-E); Reese (1984, Fig. 22 F-G); Nyholm (1986, Fig. 18 E); Frahm and Frey (1987a, Fig. 50 18); Noguchi (1987, Fig. 55 A).

Habitat. Moist travertine river bank; 1737 m.

Distribution in Central America. GUATEMALA. Quiche: Sharp 2456 (FH).

World range: Subarctic America, Western and Eastern Canada, Northwestern, North-Central, Northeastern, Southwestern, South-Central, and Southeastern U.S.A.; Mexico; Central America; Caribbean, Western South America; Northern, Southwestern, Middle, East, and Southeastern Europe; Western Asia, Caucasus, Soviet Middle Asia, Siberia, Soviet Far East, China, Eastern Asia.

Anisothecium varium is recognized by its erect to erect-spreading, lanceolate leaves, entire, recurved leaf margins, firm-walled, elongate leaf cells, and papillose peristome teeth. Although frequently illustrated with striate-papillose peristome teeth, in all material I examined the teeth are uniformly papillose.

The collection Bartram (1949) cited for this species from Guatemala (Sharp 2948) is Dicranella hilariana. Bartram (1949) cited Sharp 2948 under both D. subinclinata and D. varia.

The flexuous seta in this species appears to be a weak expression of a cygneous seta.


Plants small, terrestrial, gregarious or in tufts and mats; stems erect, simple or sparsely branched, radiculose at base. Leaves distant and reduced below, upper leaves crowded, erect-appressed to spreading or curved-secund, erect or clasping at base, gradually or abruptly narrowed above to a linear or subulate limb; margins plane or recurved, entire below and denticulate at apex, or serrulate throughout; costa single, stout, percurrent or excurrent; cells linear to subquadrate, smooth, firm-walled, not pitted, alar cells not differentiated. Dioicus. Setae elongate, erect, straight or flexuous; capsules globose to cylindrical, erect or curved, smooth or ribbed when dry, struma present or absent; stomata absent; annuli large, compound, revoluble or imperfect, of several rows of small, quadrate, loosely coherent cells variously persistent at the capsule mouth after dehiscence; opercula conic-rostrate; peristome teeth 16, reddish, short or elongate, undivided or divided to below the middle into 2 papillose forks, dorsal lamellae striate papillose or irregularly papillose. Calyptrae cucullate, entire at base. Spores lightly roughened to densely papillose to warty.

Grout (1936) lectotypified Dicranella with a species of Anisothecium, but this choice can be rejected since it was a mechanical selection using Canon 15 of the International Code of Botanical Nomenclature (Greuter et al. 1988).

Microdus differs from Dicranella in having reduced, irregularly papillose peristome teeth and warty spores. Most peristomes in Dicranella are well-developed and have papillae arranged in distinct rows, but some species have reduced, weakly striate-papillose peristome teeth. There is a complete series of intermediates between the typical Microdus and Dicranella peristomes, both genera have species with warty spores. Microdus is treated as a synonym of Dicranella here.

Dicranella is a member of a generic complex whose internal boundaries are based solely on sporophytic features. Generic relationships are blurred by the reticulate distribution of sporophytic character states (see Table 1). Character expression is variable in the group, i.e., consistently expressed in one genus but variable in another.

Table 1. Distinguishing features of the Dicranella-complex. Character states: stomata, - absent, + present; seta, s straight, f flexuous, c cygneous; annulus, + complex and revoluble, - simple and adherent; spores, p papillose, w warty; peristome, s striate-papillose, p papillose, i inserted at mouth, b on basal membrane.

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<tr>
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<th>Stomata</th>
<th>Seta</th>
<th>Annulus</th>
<th>Spores</th>
<th>Peristome</th>
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<tr>
<td>Dicranella</td>
<td>-</td>
<td>s/f</td>
<td>+/-</td>
<td>p/w</td>
<td>s, i/b</td>
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<tr>
<td>Microdus</td>
<td>-</td>
<td>s</td>
<td>+</td>
<td>p/w</td>
<td>p, i</td>
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</table>
Anisothecium + s/f − p s/p, b
Campylopodium + c + p s, i

(Not in Central America)
Microcampylopus − c + w s, i
Aongstroemia + s + p p, i

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1. Peristome teeth striate-papillose

2. Peristome teeth irregularly papillose

2. Upper leaves gradually narrowed from a lanceolate base; annulus simple, persistent
   3. D. heteromalla

3. Upper leaves triangular, ovate or oblong at base; annulus compound and revoluble

3. Leaves triangular at base, not or weakly clasping

4. Leaves ovate to oblong at base, distinctly clasping

4. Leaves short, lanceolate, gradually tapered to the apex; costa percurrent; upper leaves rounded at apex, lower margins recurved
   4. D. hilariana

2. D. harrisii

4. Leaves long, linear-lanceolate, abruptly contracted to the apex; costa excurrent; upper leaves sharply acute to acuminate at apex, lower margins plane

5. Peristome teeth < 300 um; spores warty; capsules erect, not strumose
1. D. brachyblepharis

5. Peristome teeth > 350 um; spores thickly papillose to warty; capsules inclined, strumose

7. D. standleyi

6. Leaves lanceolate; costa percurrent to subpercurrent; spores papillose

5. D. lindigiana

6. Leaves linear-lanceolate; costa excurrent; spores warty

6. D. longirostris

Mexico, near Xalapa, Deppe & Schiede (NY).

Plants dark green to yellow-green; stems 5-10 (~15) mm high. Leaves 1.5-4.0 mm long, basal leaves lanceolate, gradually narrowed to the apex, upper leaves and perichaetial leaves large, ovate-lanceolate, abruptly narrowed above a clasping base; margins plane or weakly recurved, entire below, serrulate at apex; costa percurrent in lower leaves, excurrent in upper leaves; cells rectangular, firm-walled. Setae flexuous to straight, yellow, 4-7 mm long; capsules oblong, symmetric or nearly so, smooth, dark red, 0.7-1.0 mm long; opercula conic at base, obliquely rostrate above; annuli compound and revoluble; peristome teeth red below, hyaline above, vertically papillose-striate below on outer surface, papillose above, 60-300 um high, irregularly divided into unequal forks. Spores densely papillose to warty, 20-25 um.

Illustrations. Bartram (1949, Fig. 17 E-H).
Habitat. On clay banks or roadside gravel; 350-2500 m.
Distribution in Central America. GUATEMALA. Alta Verapaz: Turckheim 6653 (NY); Baja Verapaz: Hermann 26342 (F, MO, NY). HONDURAS. Comayagua: Allen 11765 (MO, TEFH); Cortes: Olson 84-45a (MO); Lempira: Allen 11190 (MO, TEFH);
Ocotepeque: Allen 14465 (MO, TEFH); Olancho: Allen 12644 (MO, TEFH); Santa Barbara: Allen 11679 (MO, TEFH). COSTA RICA. Alajuela: Crosby 3754 (MO); Cartago: Alfaro 14 (F, FH, NY, US); Heredia: Svihla 3110 (FH); Puntarenas/Alajuela: Gentry & Burger 2750D (MO); San Jose: Svihla 2938 (FH). PANAMA. Chiriqui: Nee 14129 (MO, NY, PMA, US).

World range: Mexico; Central America; Caribbean.

The lower leaves in this species are linear and gradually narrowed to the apex much like the leaves of Dicranella hilariana, D. harrisii, or D. lindigiana. But, in D. brachyblepharis the upper leaves are ovate-linear, abruptly narrowed to the apex, and variously clasping at the base, as are the leaves of D. standleyi and D. longirostris. The striate-papillose peristome teeth of Dicranella brachyblepharis distinguish it from D. longirostris, otherwise the two are inseparable. Dicranella standleyi has striate-papillose peristome teeth, but its peristome is larger, capsules inclined and strumose, and spores densely papillose to warty. Some collections of D. harrisii have weakly clasping upper leaves and so approach those of D. brachyblepharis; they are, however, never as strongly clasping as is found in this species.

Williams (1913) placed D. brachyblepharis in Dicranella section Microdus on the basis of its short peristome teeth, but the ornamentation on the teeth is the same as in Dicranella section Dicranella.
2. Dicranella harrisii

harrisii (C. Mull.) Par., Index Bryol. Suppl. 244. 1900. Type. Jamaica, Blue
Mountains Peak, Harris 10068 (NY).

Plants yellowish green to green; stems 5-10 mm high. Leaves erect-flexuous, leaves
triangular-lanceolate to ovate-lanceolate, gradually narrowed to a sharply acute or
acuminate apex, upper leaves occasionally weakly clasping at base; margins entire
below, denticulate at apex, plane or narrowly recurved; costa excurrent, nearly filling
the apex; leaf cells narrowly rectangular below, shortly rectangular above, the marginal
cells frequently thin-walled and bulging. Setae yellow when young, red at maturity, 7-
12 mm long; capsules oval, 1.0 mm erect, symmetrical; annuli compound, revoluble;
peristome teeth well developed, striate-papillose and red below, densely papillose and
hyaline above, divided to one half their length. Spores 16-20 um, densely papillose.

Illustrations. None.

Habitat. Terrestrial and on soil over rock; 150-2500.

Distribution in Central America. GUATEMALA. Quiche: Sharp 2565 (FH); San
Marcos: Svihla 2850 (F, FH); HONDURAS. Comayagua: Olson 84-64-a (MO);
Olancho: Allen 12840 (MO, TEFH); Santa Barbara: Allen 11711 (MO, TEFH); Yoro:
Allen 13595 (MO, TEFH). NICARAGUA. Chontales: Standley 8830 (F, FH); Zelaya:
Stevens 5051 (MO). COSTA RICA. Cartago: Culberson 12333 (MO); Heredia: Valerio
22 (US); Limon: Standley 37305 (F, US); San Jose: Gomez 19401 (MO). PANAMA.
Bocas del Toro: Allen 5711A (MO); Chiriqui: Croat 33275 (MO); Cocle: Folsom &
Jaslon 2667 (MO); Darien: Allen 9012 (MO); Panama: Croat 33735 (MO); San Blas
Comarca: Allen 4954 (MO); Veraguas: Nee 9907 (MO).

World Range: Central America; Caribbean.

Dicranella harrisii is a Caribbean species first reported from Central America by
Bartram (1951). It has generally gone unrecognized, and a critical examination of additional Central American material will likely prove it to be a common species in the region. The species has short, triangular lower leaves, but upper leaves near the perichaetia clasping and abruptly narrowed to the apex as is seen in D. standleyi, D. longirostris, and D. brachyblepharis. From the latter two species it is distinguished by its well-developed peristome teeth. Dicranella standleyi has tightly clasping leaves throughout, inclined, strumose capsules and densely papillose to warty spores.

Dicranella harrisii is often confused with Dicranella hilariana, but that species has upper leaves with obtuse leaf apices, percurrent costa, and more or less plane leaf margins. The leaf marginal cells in D. harrisii have a tendency to be thin-walled and bulging in a way similar to those of Anisothecium rufescens.


Plants dark green; stems 10-20 mm high. Leaves 2-3 mm long, erect-flexuous to curved-secund, lanceolate to narrowly ovate-lanceolate, gradually narrowed to the apex; margins plane, entire below, serrulate above; costa excurrent, filling most of the upper leaf blade; cells rectangular to elongate-rectangular, firm-walled. Setae yellow, 5-15 mm long; capsules suberect or asymmetric and curved, 1.0-2.0 mm long, ovoid to cylindric; stomata absent; opercula 1.0 mm long, conic at base, long-rostrate above; annuli imperfect, of a single row of small thick-walled cells adhering to the capsule mouth after dehiscence; peristome teeth 400-500 um long, divided halfway to the base into two hyaline, papillose forks, in lower 1/2 red and strongly striate-papillose, occasionally arising from a very low basal membrane. Spores 14-18 um, lightly roughened.

Illustrations. Husnot (1884, Pl. 8); Grout (1904, Pl. 11); Jennings (1951, Pl. 11); Nyholm (1954, Fig. 15 K; 1986, Fig. 21 B); Lawton (1971, Pl. 25 9-13); Smith (1978, Fig. 62); Crum and Anderson (1981, Fig. 72 E-I); Ireland (1982, Pl. 77); Crum (1983, Fig. 27 A-B); Reese (1984, Fig. 22 C-E); Noguchi (1987, Fig. 59).

Habitat. On dead tree trunks and on bare soil; 800-2700 m.

Distribution in Central America. HONDURAS. Comayagua: Allen 11032 (MO,
A widespread Northern Hemispheric moss, Dicranella heteromalla is recognized by its lanceolate, curved-secund leaves that gradually narrow to the apex, its curved capsules and its long, striate-papillose peristome teeth. Dicranella standleyi has a similar peristome but differs in having clasping, ovate-lanceolate leaves, a compound, revoluble annulus and coarsely papillose to warty spores. The Central American collections of D. heteromalla do not have capsules nearly as distinctly curved as is commonly encountered in North America.

This is the only Dicranella in Central America that lacks a compound revoluble annulus. Furthermore, the peristome at times appears to be borne on a very short basal membrane (see illustrations in Ireland, 1982). These character states (simple, persistent annulus and peristomial basal membrane) are two features of the genus Anisothecium, but unlike that genus the capsules of D. heteromalla lack stomata.

4. Dicranella hilariana 5. Dicranella lindigiana


Plants dull green to yellowish green; stems 3-25 mm high. Leaves erect-flexuoso to subsecund, narrowly lanceolate, gradually tapered to a broadly rounded or obtuse apex; margins narrowly recurved, entire below, serrulate at apex; costa percurrent; upper leaf cells subquadrate to short rectangular; lower cells rectangular, cells variably firm- or lax-walled. Perichaetial leaves not different from upper stem leaves. Setae yellowish, becoming red with age, straight or flexuous, 0.5-1.57 cm long; capsules erect, ovoid to subcylindrical, 0.75-1.0 mm long; annuli compound, revoluble; opercula 0.75-1.0 mm long, obliquely rostrate; peristome, 250-350 um high, striate-papillose and red below, papillose and hyaline above, divided more than halfway to the base. Spores 16-20 um papillose.

Illustrations. Montagne (1839, Pl. 14); Sullivant (1864, Pl. 20, as Dicranum debile); Bartram (1949, Fig. 16 A-C, as D. subinclinata; Fig. 17 A-D); Breen (1963, Pl. 18); Crum and Anderson (1981, Fig. 68 F-M); Reese (1984, Fig. 22 H-I).

Habitat. On soil and clay, frequent on road banks and disturbed sites; 20-1784 m.
Distribution in Central America. BELIZE. Toledo: Robertson (NY).
GUATEMALA. Baja Verapaz: Sharp 2944 (FH, US); El Progreso: Sharp 5079 (FH);
Izabal: Jones & Facey 3415 (MO); San Marcos: Dwyer 15232 (MO). HONDURAS.
Atlantida: Standley 54027 (F, FH, US); Cortes: Allen 14413 (MO); Morazan: Standley 17365 (F); Yoro: Allen 13672 (MO). COSTA RICA. Cartago: Alfaro 276 (FH);
Heredia: Valerio 470 (FH); Limon: Gutierrez s.n. (FH, US); Puntarenas: Koch 5008 (FH, US); San Jose: Grayum 9677 (MO). PANAMA. Bocas del Toro: Allen 5241 (MO); Canal Area: Standley 31797 (FH, US); Chiriqui: Allen 5513 (MO); Cocle: Tyson 2472U (NY); Darien: Croat 37960A (MO); Panama: Allen 4916 (MO);
Veraguas: Witherspoon 8837 (MO).

World range: Southeastern and South-Central U.S.A.; Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

This species is characterized by its upper leaves that are broadly lanceolate and triangular at base and obtuse or broadly acute apices and narrowly recurved margins. The combination of triangular leaf bases and obtuse leaf apices separates it from all others. When its upper leaves do not have broadly rounded apices the species can be confused with Dicranella harrisii, which has sharply acute leaves, more or less plane leaf margins with thin-walled and bulging marginal cells, and upper leaves, near the perichaetia, distinctly clasping.

Plants yellowish green; stems 5-7 mm high. Leaves erect-flexuous when dry, lanceolate or narrowly oblong-lanceolate, gradually narrowed from the base to the apex, narrowly obtuse to acute; margins entire and narrowly recurved below, serrulate and plane above; costa strong, percurrent or ending at the apex; cells rectangular below, subquadrate or short rectangular above, with thin or firm walls. Setae erect-flexuous, yellow, 4-7 mm long; capsules erect, symmetric globose to ovate (rarely sub-oblung), 0.5-0.7 mm long; annuli large, compound, revoluble; opercula obliquely rostrate, 0.5 mm long; peristome teeth red to reddish brown, papillose, to 120 um high, irregularly divided. Spores 16-22 um, papillose.

Illustrations. Breen (1963, Pl. 19 1-7, as D. sphaerocarpa); Crum and Anderson (1981, Fig. 68 A-E, as D. sphaerocarpa).

Habitat. On soil; 950-800 m.


World range: Southeastern U.S.A.; Mexico; Central America; Caribbean, Western South America.

Dicranella lindigiana is better known as Dicranella sphaerocarpa, a species with globose to sub-globose capsules. But this feature is not consistently expressed: even the type collection of D. sphaerocarpa has some ovate capsules. The species has lanceolate leaves that are gradually narrowed to the apex, a percurrent costa, short, poorly developed, papillose peristome teeth, and lightly papillose spores. In leaf shape it is similar to D. hilariana, which has well developed striate-papillose peristome teeth. Dicranella longirostris has similar peristome teeth but differs in having densely papillose to warty spores and the ovate-lanceolate, somewhat clasping leaves are abruptly contracted to the apex.

The leaves of D. lindigiana may have obtuse apices, a feature emphasized by Williams (1913). However, acute apices are nearly as common in the species. For this reason, it seems likely that Dicranella barbensis will prove to be synonymous.

longirostris (Schwaegr.) Brid., Musco. Recent. Suppl. 4: 51. 1819. Weissia
longirostris (Schwaegr.) C. Mull., Syn. Musc. Frond. 1: 421. 1848. Microdus
longirostris (Schwaegr.) Schimp. ex Besch., Mem. Soc. Sci. Nat. Cherbourg 16:
162. 1872. Type. Guadeloupe, in monte sulphurifero, Richard.

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6. Dicranella longirostris               7. Dicranella standleyi

Dicranella pseudolongirostris Card., Rev. Bryol. 36: 68. 1909. Type. Mexico, Morelos,
near Cuernavaca, Pringle 10661 (MO).
Dicranella sharpii Bartr., Bryologist 50: 202. 1947. Type. Guatemala, Quiche, below Nebaj,
Sharp 2448 (FH, holotype; NY, US, isotypes). Paratype. Guatemala, Baja Verapaz,
Civija, Sharp 5188 (F, FH) [synonymous with D. brachyblepharis.]

Plants greenish brown to yellow; stems 5-10 mm high. Leaves erect-spreading, to 1
lower leaves lanceolate to oblong-lanceolate, gradually narrowed to the apex, upper leaves oblong to ovate-lanceolate, abruptly narrowed to the apex, frequently lanceolate-subulate, at times loosely clasping the stem; apex sharply acute; margins entire, plane or somewhat recurved above; costa excurrent; leaf cells rectangular below, narrow above, firm-walled throughout. Setae 5-7 mm long, yellowish to yellow-red; capsules 1.0-1.5 mm long, oblong, erect; annuli compound, revoluble; opercula obliquely long-rostrate; peristome teeth red, papillose, 120-200 um high, irregularly divided, becoming red with age. Spores 16-20 um, thickly papillose or warty.

Illustrations. Schwaegrichen (1823, Pl. 117, as Weissia longirostris); Bartram (1949, Fig. 16 G-J, as D. sharpii).

Habitat. On soil banks; 1520-3550 m.


World range: Mexico; Central America; Caribbean, Brazil.

This species has ovate to oblong-lanceolate upper leaves that are abruptly narrowed to the apex and moderately clasp the stem, short, papillose peristome teeth, and warty to thickly papillose spores. It may be confused with Dicranella brachyblepharis or D. standleyi, which have similarly shaped upper leaves. From the former it is distinguished only by its peristomial ornamentation. In D. brachyblepharis the poorly developed peristome is striate-papillose. Dicranella standleyi is a larger species with well developed, striate-papillose peristome teeth and inclined, strumose capsules.

Bartram (1947, 1949) considered this species (as Dicranella sharpii) distinct from D. alpina by its longer peristome teeth (200 um vs. 100 um) and abruptly narrowed, oblong-setaceous leaves with excurrent costa. The peristome in D. longirostris spans the variation between these two taxa, and the leaf shape cited for D. alpina does not differ significantly from that of D. longirostris. I suspect the two are the same.

Plants yellowish green, medium sized for the genus; stems 5-25 mm high. Leaves dimorphic, lower leaves lanceolate, erect spreading, non-clasping, gradually narrowed to the apex; upper leaves obovate to oblong-lanceolate, spreading-recurred, strongly clasping, abruptly narrowed to a flat, setaceous point; margins plane below, recurved at midleaf and flat above, entire below, serrulate above; costa excurrent, occupying nearly the entire upper leaf lamina; lower leaf cells long rectangular, firm-walled; upper cells short-rectangular. Setae yellow becoming red with age, 7-10 mm long; capsules oblong, strumose, erect or inclined, 1.0-1.5 mm long, smooth when dry; annuli compound, revoluble; opercula obliquely rostrate, 1.5 mm long; peristome teeth well developed, 350-400 um long, red and striate-papillose below, hyaline and densely papillose above. Spores 18-20 um, thickly papillose to warty.

Illustrations. Bartram (1928, Fig. 1 A-F).

Habitat. Terrestrial, on bare soil; 600-2050 m.

Distribution in Central America. GUATEMALA. Jutiapa: Steyermark 31938 (F). HONDURAS. Olancho: Allen 12880 (MO, TEFH). COSTA RICA. Alajuela: Crosby 3772 (MO); Cartago: Crosby & Crosby 6323 (MO); Heredia: Standley & Valerio 50086 (NY, US); Alajuela/Puntarenas: Gentry & Burger 2750F (MO). PANAMA. Bocas del Toro/Chiriqui: Folsom 4859 (MO); Chiriqui: D'Arcy 10992A-1 (MO).

World range: Central America.

Bartram (1949) synonymized this species with Anisothecium vaginatum, but D. standleyi has a compound revoluble annulus, peristome teeth inserted below the mouth, and lacks stomata. Both taxa have obovate-lanceolate upper leaves that are abruptly contracted and clasp the stem, but the leaves in Dicranella standleyi are never as tightly and smoothly clasping as is found in A. vaginatum.

Dicranella standleyi is also distinguished by its yellow setae, oblong, inclined, strumate capsules, well developed striate-papillose peristome teeth, and thickly
papilllose to warty spores. The species may be confused with D. longirostris, D. brachyblepharis, or D. harrisii, all of which have ovate-lanceolate upper leaves that are abruptly narrowed to the apex. From the first two species D. standleyi is separated by its inclined, strumose capsules and well developed peristome teeth. From D. harrisii it is distinguished by its yellow setae, oblong, inclined, strumose capsules, and thickly papilllose to warty spores.

The leaf dimorphism in this species is particularly striking. If only lower leaves are examined, it may even be confused with D. hilariana.

Excluded species

Dicranella alpina (C. Mull.) Par.
This species was reported from Guatemala by Bartram (1949) on the basis of two specimens (Naguala, Bernoulli & Cario 64, the type, and Alta Verapaz, Turckheim 6653). The first I have not examined, but the second is D. hilariana. From its description it appears to be the same as D. longirostris.

Dicranella barbensis Ren. & Card.
Type material was not examined. From its description it appears to be D. lindigiana.

Dicranella herminieri Besch.
This is a Caribbean species that Florschutz (1964) considered the same as D. hilariana. All Central American material named D. herminieri that I examined can be assigned to D. hilariana.

Dicranella lagunaria (C. Mull.) Par.
Known only from the type (Guatemala, Laguna del Pino, Bernoulli & Cario 116), Williams (1913) suggested this species was the same as D. brachyblepharis.

Dicranella perrotetii (Mont.) Mitt.
Reported from Costa Rica (Bartram 1951) and Panama (Williams 1911). I have not examined the specimens on which the Costa Rican records are based; the Panamanian record (Williams 1058, NY) is D. hilariana.


Plants small, similar in habit and appearance to Dicranella. Leaves broadly ovate, sheathing at base abruptly subulate above; costa less than 1/3 the leaf width at base, filling the subula, excurrent; alar cells not differentiated. Setae flexuosus to cygneous; capsules ovoid to cyclindrical; stomata absent; peristome teeth 16, split to middle; opercula rostrate. Calyptrae cucullate, entire. Spores densely papillose to warty.

This genus, a member of the Dicranella-complex, differs from Campylopodium and Dicranella by a single sporophytic feature. Microcampylopus has cygenous setae and lacks stomata. Campylopodium has similar setae but has stomata, while Dicranella has straight to flexuous setae and lacks stomata. Microcampylopus has been considered distinct in having warty spores, but this condition is found in Dicranella.


Plants, gregarious, yellowish green, terricolous; stems dimorphic, male plants slender, to 8 mm high, female plants 5-10 mm long; central strand small. Leaves evenly spaced, spreading, flexuosus, leaves on male plants and the lower leaves on
female plants lanceolate from an oblong, clasping base gradually narrowed and subulate above; upper leaves on female plants 2.5-4.0 mm long, from a short, broadly ovate, sheathing base, abruptly narrowed into a long subula; margins plane above, entire; costa in cross section with a median row of guide cells, ventral and dorsal stereid bands; upper cells rectangular to rhomboidal thick-walled, basal cells of leaves on male plants and lower leaves of female plants quadrate, rectangular on upper leaves thick- to firm-walled. Dioicous. Setae 3-7 mm long, yellowish to brown, smooth; capsules exserted, ovoid to cylindrical, 1.0-1.5 mm long, sometimes ribbed when dry; annuli present; stomata absent; peristome red below, yellowish white above, teeth lanceolate, vertically striate below, papillose above; opercula 1 mm long. Calyptrae 1.0-1.5 mm long.

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Microcampylopus leucogaster

Illustrations. Bartram (1949, Fig. 17 I-K, as Campylopodium pusillum); Giese and Frahm (1985, Figs. 5, 10-22, 45, as M. curvisetus); Frahm (1991, Figs. 1 F, 4 C, 6 B, 8 D, 146, as M. curvisetus).

Habitat. On soil of road banks, occasionally epiphytic; 900-2700 m.

Distribution in Central America. BELIZE. Cayo: Davidse & Brant 33056 (MO).
GUATEMALA. Alta Verapaz: Turckheim 6651 (NY); Baja Verapaz: Sharp 5188 (F); Huehuetenango: Sharp 4878 (F, FH); San Marcos: Standley 86515a (F, FH); Quezaltenango: Sharp 2022 (FH, US); Quiche: Sharp 2356a (F, FH, MO).
HONDURAS. Comayagua: Allen 12320 (MO, TEFH); Cortes: Allen 14197 (MO, TEFH); Ocotpeque: Allen 14425 (MO, TEFH); Olancho: Allen 12867 (MO, TEFH).
NICARAGUA. Jinotega: Stevens 17845 (MO). COSTA RICA. Alajuela: Alfaro 52a (FH); Cartago: Gomez 19395b (MO); San Jose: Crosby & Crosby 6400 (MO).
PANAMA. Chiriqui: Salazar 538 (NY).

World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

Microcampylopus leucogaster is essentially a Dicranella with cygneous setae; collections that lack sporophytes can only be tentatively named. The smaller size, narrower costa, undifferentiated alar cells, and broadly clasping leaves that are abruptly narrowed into a long subulate point filled by the costa will distinguish this species from Campylopus, another genus with cygneous setae. Dicranella brachyblepharis and D. longirostris are similar in having ovate, clasping leaf bases that are abruptly narrowed to long subulae. Dicranella brachyblepharis has shorter upper leaf cells, while D. longirostris differs gametophytically only in having a weaker costa and broader, less sharply pointed leaves.

Giese and Frahm (1985) synonymized Dicranum leucogaster and Aongstroemia curviseta. They chose the epithet curvisetus for the combined species in Microcampylopus, but leucogaster is the older name.

Plants small, in loose to compact tufts; stems radiculose. Leaves erect-patent, appressed or slightly secund, narrowly acuminate; costa broad, to 2/3 the leaf width at base, excurrent, in cross section with large ventral and dorsal hyalocysts, a median band of stereid cells and a small group of ventral stereids; cells firm-walled, linear or rectangular to subquadrate, smooth; alar cells weakly developed. Setae yellowish, becoming brownish with age, erect; capsules erect, cylindrical, smooth, yellowish; exothecial cells elongate; stomata absent; annuli well developed and revoluble; opercula long rostrate; peristome divided nearly to the base, papillose throughout or striate-papillose at base. Calyptrae cucullate, entire at base.

*Campylopodiella* is similar to small members of *Campylopus*, *Dicranodontium*, *Dicranella*, or *Ditrichum*. Recognition of the genus depends on the examination of leaf cross sections. In transverse section the broad costa consists of a small pocket of ventral stereids, a layer of ventral hyalocysts, a median band or groups of stereid cells, and a dorsal layer of hyalocysts. *Brothera*, the only other moss genus with a costal cross section similar to *Campylopodiella*, lacks ventral costal stereids, and has entire to perforate peristome teeth and a broader costa.

*Campylopodiella* has been treated by Takaki (1971, 1973), Frahm (1984), and Muller and Frahm (1987).

1. Median leaf cells short rectangular, basal cells firm-walled; alar region weakly bulging; plants with terminal, blackish jointed flagella
   1. *C. flagellacea*

1. Median leaf cells elongate-rectangular, basal cells thin-walled and lax; alar region not bulging; plants without terminal flagella
   2. *C. stenocarpa*

Malaga, Herzog 4367 (NY).

Plants tufted, yellowish green; stems erect, 3-15 mm long. Leaves evenly spaced, erect-patent to appressed, concave, lanceolate, 1.5-2.5 mm long, oblong below, narrowly acuminate above; margins entire and erect below, incurved above, minutely serrulate at extreme apex; costa 1/2-2/3 the leaf width at base, excurrent; upper cells short rectangular to quadrate, firm-walled, basal cells rectangular to subquadrate, hyaline, firm-walled, those at margins somewhat longer and narrower but not forming a distinct border; alar cells in small, weakly auriculate groups, slightly inflated and at times poorly developed. Asexual reproduction by deciduous flagella at the stem tips, the flagella becoming black and necrotic in the area of separation from the stem, the stem remaining black-tipped after the flagella are lost; flagellate leaves short, with broader costa, leaf cells quadrate and more firm-walled and the leaf apices narrowly obtuse. Dioicous. Perichaetial leaves suddenly contracted from a broadly ovate base. Setae 10-13 mm long; capsules 2 mm long; peristome yellow, teeth lanceolate, papillose, cleft to the base, 0.3-0.4 mm high; opercula 1.0-1.2 mm long. Calyptrae 2.5-3.0 mm long, smooth. Spores 12 μm, rounded, smooth to lightly papillose, yellow.

Illustrations. Herzog (1916, as Campylopus malagensis Pl. 1 6); Frahm (1978, Pl. 16, as Campylopus malagensis); Frahm (1979a, Fig. 1, as Campylopus malagensis); Muller and Frahm (1987, Pl. 2 1-7, as Campylopoediella malagensis); Frahm (1991a, Fig. 161).

Habitat. On fallen logs, non-calcareous boulders and soil at base of trees; 2134-3383 m.
Distribution in Central America. GUATEMALA. Huehuetenango: Standley 81635 (F, FH); San Marcos: Sharp 5462 (F). PANAMA. Chiriqui: Allen 9172 (MO).
World range: Mexico; Central America; Western and Northern South America.

Synonymized with Campylopodiella stenocarpa by Padberg and Frahm (1985) and Muller and Frahm (1987), this species differs in its dioicous condition, firm-walled basal leaf cells, sub-rectangular to quadrate median leaf cells, and weakly auriculate alar region. In C. stenocarpa the plants are autoicous with perigonia terminal on short branches below the perichaetia, the median leaf cells are elongate-rectangular, the basal leaf cells are enlarged, thin-walled and lax, and the alar region is non-auriculate. A notable feature of C. flagellacea is its deciduous, stem-tip flagella. The flagella are shed by necrosis, which causes a blackening in the area of separation. The species can be recognized even after the flagella have been shed by the presence of blackened stem tips. The flagellate leaves are shorter, have broader costae, more obviously quadrate and thick-walled leaf cells, and narrowly obtuse leaf apices.

Metzleria tuerckheimii Broth. in Card., Rev. Bryol. 38: 100. 1911, nom. nud. Based on Guatemala, Alta Verapaz, Coban, Turckheim (NY); Cubilguitz, Turckheim.

Plants yellowish green, stems erect, 8-15 mm long. Leaves evenly spaced, appressed to somewhat secund or spreading above when dry, concave, stem leaves lanceolate from a short ovate base narrowed into a long acumen, 3.0-7.0 mm long, apex subulate; margins incurved, entire below, weakly serrulate at the apex; costa to 1/3 the leaf width at base, excurrent, smooth; upper cells elongate to linear, homogeneous, thick-walled, smooth; basal cells rectangular, hyaline, thin-walled, those at the margins longer, narrower, and firm-walled forming a distinct border; alar cells weakly differentiated, frequently fugacious, hyaline or red-brown, thin-walled. Autoicous. Perigonia terminal on short branches below the perichaetia. Setae 7-20 mm long; capsules 2.5-3.0 mm long; peristome yellowish, teeth lanceolate, striate at base,
papillose above, cleft nearly to the base; opercula 1.0–1.5 mm long. Calyptrae 2.0–3.0 mm long, smooth. Spores 11–13 μm, lightly papillose, yellow-green.

Illustrations. Bartram (1949, Fig. 23 D–F, as Atractylocarpus costaricensis);

Padberg and Frahm (1985, Figs. 64–70, as Atractylocarpus stenocarpus); Muller and Frahm (1987, Pl. III 1–8); Frahm (1991a, Fig. 163).

Habitat. On tree trunks and decaying logs (frequently on pine and juniper in Guatemala and Honduras), occasionally on shaded banks and wet rocks; 1080–3300 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: Turckheim (NY); Baja Verapaz: Sharp 2691 (MO, US); Chimaltenango: Standley 57827a (F, FH); El Progreso: Steyermark 43436 (F, FH, US); Jalapa: Steyermark 32493 (F, FH, NY); Quetzaltenango: Sharp 2114 (MO); Quiche: Richards et al. 3082 (F, MO, NY); Sacatepequez: Standley 65223a (F, FH); San Marcos: Sharp (US); Tontonicapan: Standley 84535 (F, FH, NY, US). EL SALVADOR. Santa Ana: Watson 101 (MO).

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2. Campylopodiella stenocarpa
1. Campylopus albidovirens

HONDURAS. Comayagua: Standley 56399 (F, FH, NY, US); El Paraiso: Rodriguez
1747 (F, MO); Intibuca: Standley 25411 (F); Lempira: Allen 11184 (MO, TEFH); Morazan: Standley & Molina 4307 (F, FH). NICARAGUA. Granada: Miller et al. 1417 (MO). COSTA RICA. Alajuela: Crosby & Crosby 6270 (MO); Cartago: McDaniel 6753 (NY); Heredia: Gomez 21307 (MO, NY); Limon: Gutierrez 202 (F); Puntarenas: Davidse et al. 28526 (MO); San Jose: Gomez 20059 (MO). PANAMA. Chiriqui: Croat 26896 (MO).

World range: North-Central U.S.A.; Mexico; Central America.

Marked by its autoicous condition, elongate median leaf cells, thin-walled, hyaline basal cells, and lack of flagellate stem tips, Campylopodiella stenocarpa is a common Central American species that may be confused with Ditrichum because of its small size and deeply divided peristome teeth. The small leaves are difficult and tedious to section, but an examination of its costa in cross section and its autoicous sexual condition makes the species unmistakable.


Plants small to robust, densely tufted; stems sparsely branched, often densely tomentose; leaf rhizoids frequently on the lower dorsal surface of the costa; in cross section with a well-developed central stand. Leaves ovate-lanceolate to ovate-subulate, variably toothed, nearly always denticulate at the extreme apex; costa broad, occupying most of the upper leaf, percurrent to excurrent, often ribbed or mammillose at back, at times with multi-cellular lamellae; cells smooth, porose or entire, upper cells quadrate, oval, rhombic, oblong, rhomboidal or elongate, usually in oblique rows, incrassate, marginal cells at base at times forming a hyaline border; alar cells commonly well-developed. Dioicous. Setae cygneous when moist; capsules exserted, ovoid to ellipsoid, strumae present or absent, erect or curved; stomata absent; annuli present; peristome teeth 1/2 to nearly their full lengths divided into two filaments, generally striate on the outer surface; opercula rostrate. Calyptrae cucullate, entire or fringed at base by long, single-celled hairs. Spores yellow to brown, variously papillose.

Campylopodiella is a large, taxonomically complex group of worldwide distribution.
Due to great variation in nearly all its characters the generic limits of the genus are diffuse. In general, Campylopus consists of medium to large, dioecious mosses with stiff, erect to spreading (generally unbordered), linear leaves having broad, excurrent costa approximately 1/2 to 2/3 the leaf base width. Many species have costae with a ventral layer of variously enlarged hyaline cells (hyalocysts). Sporophytically, the cygneous setae, capsules that lack stomata, and dicranaeous peristome teeth are distinctive. The calyptrae are cuculate and frequently ciliate at base.

In the typical sense Campylopus is easy to recognize, but the genus harbors species whose characters grade into those of Atractylocarpus, Dicranodontium, Dicranella, Campylopodium, Paraleucobryum, and Pilocopon (see Allen 1989). In the following treatment Campylopus is divided into two groups on the basis of the form of the costal cells ventral to the guide cells.

1. Ventral stereids present in costa or if absent guide cells exposed ventrally
   Key A
   1. Ventral hyalocysts present in costa
      Key B

Key A. Campylopus with ventral stereids or guide cells ventrally exposed

1. Plants with clusters of brood bodies
   2
1. Plants without brood bodies
   3

2. Basal leaf cells at margins non-porose and quadrate; costa spurred above, mammillose at back
   21. C. savannarum
2. Basal leaf cells at margins long-rectangular, generally porose, especially toward the costa; costa not spurred, smooth at back
4. C. arctocarpus

3. Leaves with hyaline hair points
   4.

3. Leaves without hyaline hair points
   6.

4. Leaf cells non-porose; marginal cells quadrate
   21. C. savannarum

4. Leaf cells strongly porose; marginal cells linear to rectangular
   5.

5. Leaves 3-8 mm long, basal border of elongated, hyaline cells absent; alar cells not in excavate groups; costal ventral stereids commonly absent, the guide cells ventrally exposed
   20. C. richardii

5. Leaves 7-13 mm long, basal border of elongate, hyaline cells present; alar cells in bulging, excavate groups; costal ventral stereids well developed
   26. C. valerioi

6. Upper leaf cells quadrate
   7.

6. Upper leaf cells oval to oblong-rhomboidal
   8.

7. Leaves 8-13 mm long; basal cells strongly porose; stems with comal tufts
   27. C. weberbaueri

7. Leaves 5-8 mm long; basal cells non-porose or very weakly porose; stems without comal tufts
   7. C. atlanticus

8. Basal leaf cells at margins non-porose and quadrate
21. C. savannarum
8. Basal leaf cells at margins porose and rectangular to elongate-rectangular

9. Leaves at base with a short, hyaline border, most leaves over 10 mm long; all cells strongly porose; plants with comal tufts

26. C. valerioi
9. Leaves elimbate, 3-7 mm long; cells moderately porose at base only; plants without comal tufts

4. C. arctocarpus

Key B. Campylopus with ventral hyalocysts

1. Plants with brood leaves or brood buds

2. Plants without brood leaves or brood buds

6

2. Plants with masses of stalked brood leaves

3. Robust plants with firm-walled basal cells

6. C. asperifolius
3. Small plants with lax, thin-walled, bulging basal cells

11. C. fragilis

4. Leaves not bordered at base; costa with dorsal stereids; ventral hyalocysts smaller or equal to the guide cells

10. C. flexuosus
4. Leaves bordered at base by elongate, hyaline cells; costa without dorsal stereids or with pseudostereids; ventral hyalocysts larger than the guide cells

5. Leaves broadly lanceolate, short acuminate, serrate only at the extreme apex; costa
in cross section with sharp-angled, pentagonal guide cells that interdigitate with the ventral hyalocysts; dorsal stereid absent

1. C. albidovirens

5. Leaves narrowly lanceolate, long and narrowly acuminate, ending in a sharp serrate point; costa in cross section with rounded guide cells not interdigitating with the ventral hyalocysts; dorsal pseudostereids present

5. C. areodictyon

6. Leaves with hyaline hair points; see also C. richardi in Group A

7

6. Leaves without hyaline hair points

10

7. Costa in the upper one-third with dorsal lamellae 2-3-cells high

19. C. pilifer

7. Costa smooth to mammillosse on dorsal surface

8

8. Upper leaf cells narrowly elongate

18. C. paramoensis

8. Upper leaf cells rhomboidal

9

9. Hyaline hair points present on all vegetative and perichaetial leaves

17. C. oerstedianus

9. Hyaline hair points present only on some comal leaves

24. C. surinamensis

10. Basal leaf cells porose

11

10. Basal leaf cells non-porose

17
11. Costa 2/3 or more the leaf width at base; leaves at base appearing flattened when dry
   12
11. Costa at base 1/3-1/2 the leaf width; leaves at base concave base when dry
   13

12. All basal leaf cells strongly porose; leaves with a narrow hyaline border at base;
   upper leaf cells elongate-rhombodial to linear
   23. C. subcuspidatus
12. Inner basal leaf cells porose, outer basal leaf cells nonporose; leaves elimbate;
   upper leaf cells oval
   22. C. standleyi

13. Costae 1/3 the leaf width; costa in cross section with ventral hyalocysts less than
   1.5 | the size of the guide cells
   14
13. Costa 1/2 the leaf width; costa in cross section with ventral hyalocysts to 2 | the
   size of the guide cells
   15

14. Leaves 3-5 mm long; basal juxtacostal cells enlarged, square to short-rectangular; upper leaf cells linear
   3. C. angustiretis
14. Leaves 8-14 mm long; basal juxtacostal cells not enlarged, rectangular to rhomboidal; upper leaf cells rectangular to elongate-rectangular
   13. C. hoffmannii

15. Median leaf cells quadrate to short rectangular
   2. C. anderssonii
15. Median leaf cells oblong to rhomboidal
   16
16. Leaves subulate; dry leaf apex flexuous, straight
   9. C. densicoma
16. Leaves acuminate; dry leaf apex stiffly erect and wavy or spirally twisted
   6. C. asperifolius

17. All basal cells lax, enlarged, bulging and thin-walled
   18
17. Basal cells firm-walled throughout or with a distinct border of linear, firm-walled cells
   19

18. Costa in cross section with dorsal stereid band extending the width of the costa; enlarged, hyaline basal leaf cells extending well upwards at the margin in a V-shaped pattern; alar cells moderately to weakly differentiated
   25. C. tallulensis

18. Costa in cross section with dorsal stereid bands not extending to the edges of the costa, margins of the costa consisting of 2-3 layers of enlarged, thin-walled, hyaline cells; enlarged, hyaline basal leaf cells grading evenly into or extending a little way along the margins into the quadrate median leaf cells; alar cells not differentiated
   11. C. fragilis

19. Costa in cross section with small ventral hyalocysts, smaller than or slightly larger than the guide cells
   20
19. Costa in cross section with large ventral hyalocysts, much larger than the guide cells
   24

20. Upper leaf cells linear or narrowly elongate
   3. C. angustiretis
20. Upper leaf cells quadrate, oval or rhomboidal

21

21. Leaves subulate, lamina quickly narrowed from an ovate base; juxtacostal basal cells enlarged, shortly rectangular, contrasting sharply with the narrower, longer, thicker-walled outer basal cells; capsules erect when dry
28. C. zygodonticarpus

21. Leaves lanceolate, lamina gradually narrowed, extending nearly to the apex; juxtacostal basal cells not sharply contrasting with the outer basal cells; capsules curved when dry

22

22. Upper laminal cells subquadrate
10. C. flexuosus

22. Upper laminal cells rectangular to oval

23

23. Leaf apex of upper comal leaves strongly dentate and at times subhyaline; costa dorsally mammillose above
24. C. surinamensis

23. Leaf apex smooth to weakly serrulate, concolorous; costa dorsally smooth above
15. C. lamprodictyon

24. Marginal leaf cells at base narrowly linear or laxly rectangular, forming a distinct border

25

24. Marginal leaf cells variously differentiated but not forming a distinct border

28

25. Leaves broadly lanceolate, short acuminate; costa in cross section with sharp-angled, pentagonal guide cells that interdigitate with the ventral hyalocysts; dorsal stereid cells absent
1. **C. albidovirens**

25. Leaves narrowly lanceolate, long narrowly acuminate to setaceous; costa in cross section with rounded, non-interdigitating guide cells; dorsal stereids or pseudostereids present

26

26. Leaves 10 mm or more long

8. **C. cavifolius**

26. Leaves 4-8 mm long

27

27. Leaves spreading secund when dry; upper leaf cells oblong-rectangular, 14-22 um

16. **C. nivalis**

27. Leaves stiffly erect when dry; upper leaf cells subquadrate, 5-12 um

5. **C. areodictyon**

28. Median leaf cells oblong to rhomboidal

29

28. Median leaf cells quadrate or short rectangular

30

29. Leaves subulate; leaf apex flexuous, not wavy or spirally twisted when dry

9. **C. densicoma**

29. Leaves acuminate; leaf apex stiffly erect and wavy or spirally twisted when dry

6. **C. asperifolius**

30. Costa dorsal stereid band in lower one-third of leaf not extending to the costal margins; basal marginal cells extending upward in a V-pattern

12. **C. heterostachys**

30. Costa dorsal stereid band throughout the leaf extending to the costal margins; all basal cells ending at the same level
31. Leaves more than 10 mm long and the costa over 1 mm wide at base
   14. C. jamesonii
31. Leaves 10 mm or less long and the costa less than 1 mm wide
   2. C. anderssonii


Plants slender to medium, compactly tufted, pale greenish yellow with a grayish, glossy sheen when dry; stems variably tomentose, 2–7 cm long, hylodermis present. Leaves 4–6 mm long, erect-spreading when wet, erect-falcate when dry, concave below, tubulose above, broadly lanceolate, apex short-acuminate; margins entire or toothed at apex; costa percurrent, 5/8–7/8 the leaf width at base, dorsal surface smooth or mammillose, in cross section with enlarged ventral hyalocysts, large, well developed, pentagonal-shaped guide cells, dorsal stereid band absent, cells below the guide cells enlarged, thin-walled at the margins, thick-walled near the center of the costa; upper cells quadrate to oblong, incrassate, not porose; basal cells long-rectangular, laxly thin-walled, hyaline, those at the basal margin laxly rectangular to linear, forming a distinct border; alar cells variously developed, at times hyaline and weakly developed at other times well developed, brownish red. Setae 5–7 mm long, yellow to reddish brown; capsules erect to slightly curved, striate when dry, 1.5 mm long; opercula 1 mm long. Calyptrae 2 mm long, ciliate at base. Spores 10–15 μm.

Illustrations. Herzog (1916, Pl. 1 12); Bartram (1949, Fig. 18 A–E); Frahm (1978, Pl. 2); Frahm (1982, Fig. 3 b); Frahm (1991a, Fig. 21).

Habitat. On rock and bark; 2700–3800 m.

Distribution in Central America. GUATEMALA. Chimaltenango: Standley 58745a (F); Huehuetenango: Sharp 4976 (F); Quezaltenango: Standley 86137 (F, FH);
Campylopus albidovirens is distinctive in its pale greenish yellow color (frequently grayish as in Paraleucobryum longifolium), enlarged, pentagonal guide cells that interdigitate at their apex with the ventral hyalocysts, and the absence of dorsal costal stereid cells. These character states are found in C. pittieri, which has weaker alar cell development, shorter, thicker leaves, the costa narrowed at base, and longer setae (to 14 mm long).

Campylopus albidovirens is similar to C. nivalis in color and in having dorsal pseudostereids in its costa. Campylopus nivalis has long, narrowly lanceolate leaves, entire calyptrae, and rounded, thick-walled guide cells that do not interdigitate with the ventral hyalocysts.

Campylopus longisubulatus Ther., Rev. Bryol. Lichenol. 11: 49. 1939. Type. Bolivia, Tablas, 1800 m, Herzog 4566.

Plants medium, tufted, greenish yellow, moderately shiny; stems variably white or reddish tomentose, to 6 cm long. Leaves linear, 6-10 mm long, flexuus to distinctly secund when dry, slenderly setaceous above, narrowly concave below, serrate to serrulate above; costa excurrent, 1/2-2/3 the leaf width at base, dorsal surface smooth or lightly mammillose, in cross section with enlarged ventral hyalocysts, stereid band well developed and extending to the edge of the costa; upper and median cells quadrate, 12-25 um long, incrassate, not porose; basal cells near the costa enlarged, rectangular, firm-walled, at times more or less porose, basal marginal cells narrower and more
elongate but not forming a distinct border; alar cells reddish to hyaline, moderately developed, extending to the costa, not in excavate groups and frequently fugacious. Setae 7-10 mm long, red; capsules erect to slightly curved, striate when dry, 1.5-2.0 mm long; opercula shortly rostrate, 1 mm long. Calyptrae not seen. Spores 12-15 um.

Illustrations. Bartram (1928, Fig. 6 A-I, as C. straminifolius); Frahm (1975, Fig. 1; Fig. 12, as C. insularis); Frahm (1978, Pl. 16, as C. longisubulatus; Pl. 25, as C. subinacorralis); Frahm (1991a, Fig. 24).

Habitat. On stumps, logs, tree trunks, and terrestrial on moist banks; 1400-2700 m.

Distribution in Central America. GUATEMALA. Quezaltenango: Steyermark 34325 (F, FH); San Marcos: Standley 86300 (F, FH); Zacapa: Steyermark 42660 (FH). HONDURAS. Comayagua: Allen 11029 (MO, TEFH); Cortes: Allen 14317 (MO, TEFH); Lempira: Allen 12020 (MO, TEFH); Olancho: Allen 12646 (MO, TEFH); Santa Barbara: Allen 11644 (MO, TEFH). COSTA RICA. Heredia: Crosby 10928 (MO); Puntarenas: James s.n. (US); San Jose: Standley 43016 (US). PANAMA. Bocas del Toro: Allen 5051A (MO); Chiriqui: Croat 34823 (MO).

World range: Mexico; Central America; Western and Northern South America.

Better known in Central America as Campylopus longisubulatus, this species has long, narrow leaves, costa with ventral hyalocysts and quadrate median leaf cells. Campylopus jamesonii and C. heterostachys also have this combination of characters. The former is distinguished by its wider costa and broader leaves. In C. heterostachys the leaves are flattened below when dry, the costal stereid band does not reach the margins of the costa, the basal leaf cells extend upward along the margins a short
2. Campylopus anderssonii

Distance in a V-shaped pattern, and the stem epidermal cells are somewhat inflated and thin-walled. Campylopus anderssonii and C. heterostachys are not sharply distinct in Central America, and it may be that only one taxon is represented in the region. Expressions with weakly porose basal cells near the costa resemble C. densicoma, but that species has oblong to rectangular median leaf cells.


Plants medium, tufted, yellowish green; stems weakly tomentose, 3.5-4 cm long, at times with comal tufts. Leaves 3-5 mm long, widely spaced, erect spreading dry, distinctly spreading from the base wet, concave, lanceolate, apex shortly subulate, entire below, weakly denticulate at extreme apex, concave; costa distinctly channeled, shortly excurrent, 1/3 the leaf width at base, not ridged at back, in cross section with ventral hyalocysts equal to or smaller than the guide cells, dorsal stereids well developed; cells thick-walled, upper and median cells linear, basal cells elongated rectangular, enlarged and at times porose-pitted near the costa, cells just above the alar

cells enlarged, square to short rectangular, porose-pitted; alar cells well developed, reddish to hyaline, inflated, auriculate, extending to the costa. Sporophytes unknown.
Campylopus angustiretis has linear median and upper leaf cells, concolorous leaf apices, narrow, distinctly channeled costa, and ventral hyalocysts equal to or smaller than the guide cells. The only other Central American species with linear leaf cells, C. paramoensis, has hyaline-tipped leaves and ventral hyalocysts distinctly larger than the guide cells. The presence of small ventral hyalocysts cells in this species relates it to C. surinamensis (q.v.).

   Dicranum arctocarpus Hornsch., Fl. Bras. 1: 12. 1840. Type. Brazil [Uruguay], Montevidensibus, Sellow.

   Plants medium to large, tufted, dark green to yellow-brown; stems 2-4 cm long. Leaves appressed to erect-spread (at times falcate-secund) linear-lanceolate, 3-7 mm long; lamina distinct to the acuminate apex; margins incurved above, serrate at apex; dorsal surface of costa mammillose to ribbed, ventral hyalocysts absent, ventral stereids weakly developed, dorsal stereids well developed; upper cells oval to rhomboidal, 8-25 um long, incrassate, basal cells rectangular, incrassate and pitted; alar cells red-brown, well developed, thin-walled. Brood bodies occasionally present at stem apex. Setae 8-10 mm long, red, papillose-roughened at the apex; capsules erect to curved, oblong, 2.0 mm long, ribbed when dry, neck scabrous; opercula 1.5 mm long. Calyptrae 2.5 mm long, ciliate at base. Spores 15-18 um, smooth to lightly papillose, yellow.
Illustrations. Bartram (1949, Fig. 22 A-C); Florschutz (1964, Fig. 20); Crum and Anderson (1981, Fig. 94 A-F); Frahm (1978, Pl. 1); Frahm (1991a, Figs. 5 E, 27).

Habitat. On tree branches and trunks, humus of rotting stumps and soil; 800-2300 m.

Distribution in Central America. BELIZE. Cayo: Allen 15229 (MO); Toledo: Allen 15485 (MO). GUATEMALA. Alta Verapaz: Standley 92300 (F); Huehuetenango: Standley 62586 (FH); Jalapa: Steyermark 32493a (F); Quezaltenango: Standley 66393 (MO); Quiche: Standley 62461 (FH); San Marcos: Croat 40979 (MO). HONDURAS. Comayagua: Allen 13934 (MO, TEFH); Cortes: Allen 14268 (MO, TEFH); Lempira: Allen 11270 (MO, TEFH); Morazan: Standley 4941 (F); Ocotepeque: Allen 14448 (MO, TEFH); Olancho: Allen 12642 (MO, TEFH); Yoro: Allen 13658 (MO).

NICARAGUA. Jinotega: Stevens 5649 (MO); Matagalpa: Stevens 17106 (MO). COSTA RICA. Alajuela: Crosby 3758 (MO); Cartago: Valerio 231 (US); Heredia: Standley & Valerio 50096 (NY, US); Puntarenas: Croat 47112 (MO); San Jose: Crosby 9842 (MO). PANAMA. Bocas del Toro: Allen 5291 (MO); Chiriqui: Croat 37205A (MO); Cocle: Mori & Kallunki 5296A (MO); Darien: Mori & Gentry 4347 (MO); Panama: Allen 4921 (MO); Veraguas: McPherson 12067B (MO).

World range: Mexico; Central America; Caribbean, Western, Northern, and Southern South America, Brazil.

In Campylopus arctocarpus the leaves are generally stiffly erect and the basal leaf cells are distinctly porose and incrassate, but some collections have plants with longer, more or less secund leaves, distinctly excurrent costa and weakly porose basal leaf cells. The extreme in this expression was described as C. falcatulus (Bartram 1928). This species has weakly developed ventral stereids and a tendency for the guide cells (especially toward the edges) to be flush with the outside margin, thereby forming pseudo-hyalocysts.

Campylopus arctocarpus is much like the West Indian C. cubensis Sull. (reported from Central America as C. harrisii (C. Mull.) Par.). Campylopus cubensis differs in having longer upper leaf cells, more serrate leaf, margins and more sharply lanceolate leaves. These features are variable within both species, and Central American plants named C. cubensis fall within the range of variability of C. arctocarpus.
Collections of Bryohumbertia filifolia var. longifolia that lack sporophytes will key to C. arctocarpus. However, B. filifolia is a much more slender plant with a distinct comal-tuft morphology.

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4. Campylopous arctocarpus              5. Campylopus areodictyon

Dicranum areodictyon C. Mull., Syn. Musc. Frond. 1: 394. 1848. Type. Colombia,  
Merida e Sierra Nevada, Funck & Schlim in coll. Linden 1082 (NY, isotype).  
Dicranum subconcolor Hampe, Linnaea 32: 138. 1863. Campylopus subconcolor (Hampe)  

Plants medium sized, tufted, pale green to dark greenish yellow at tips, pale yellow  
at base of leaves; stems weakly to moderately tomentose, 5-7 cm long, hyalodermis  
present. Leaves 4-5 mm long, erect-appressed to erect spreading, concave, lanceolate, 
apex narrowly acuminate to subulate, entire below, denticulate or muricate at the  
extreme apex; costa percurrent to shortly excurrent, to 5/8 the leaf width at base, in  
cross section with well-developed ventral hyalocysts, dorsal stereids absent, present in  
small patches at center of costa or consisting entirely of pseudostereids, margins of the  
costa indistinctly separated from the lamina; upper cells quadrate to shortly rectangular,  
5-12 um, incrassate, not porose; basal cells long rectangular, hyaline, thin-walled,  
marginal cells long, narrow, firm-walled, forming a limbidium 6-12 cells; alar cells  
weakly developed, red-brown to hyaline, thin-walled. Brood buds short, tumid,
occasionally in upper parts of the stem. Sporophyte not seen.

Illustrations. Frahm (1978, Pls. 2, 24, as C. subconcolor); Frahm (1980a, Figs. 17-18, as C. subconcolor); Frahm (1991a, Figs. 5b, 30).

Habitat. On soil and rocky substrates; 2900-3447 m.

Distribution in Central America. COSTA RICA. Cartago: Bowers 414A (US); San Jose: Koch 5088 (US); San Jose/Cartago: Davidse et al. 24818 (MO). PANAMA. Bocas del Toro: Gomez et al. 22508 (CR, MO); Chiriqui: Croat 34941 (MO).

World range: Central America; Western and Northern South America.

Campylopus areodictyon is easily confused with C. nivalis. Both species have weakly developed dorsal stereids in the costa (usually present as pseudostereids) and a well developed basal limbidium. Typically, C. nivalis has pale, whitish yellow, secund leaves, while in C. areodictyon the leaves are dark, greenish yellow and erect to appressed. Technically, the species are distinguished by differences in the size and shape of their upper leaf cells.

Campylopus albidovirens, also somewhat similar, has appressed, broadly lanceolate leaves that lack dorsal stereids in the costa, a pale yellow-green color, and enlarged, thin-walled, sharply angled guide cells that interdigitate with the ventral hyalocysts.

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Plants medium to large, tufted, pale green to yellow; stems moderately red-tomentose, to 4 cm long. Leaves 4-6 mm long, erect-patent when dry, frequently with stiffly erect and wavy to twisted apex, erect-spreading when wet, lanceolate, ovate at base, concave below, serrate at the apex, at times serrulate in the upper 1/4; costa shortly excurrent, concolorous, 1/3-1/2 the leaf width at base, smooth or lightly mammillose on dorsal surface, in cross section guide cells well developed, ventral hyalocysts larger than guide cells, dorsal stereids well developed; median and upper cells obliquely rhomboidal, 12-20 um long, all cells firm-walled, not porose (rarely with a few juxtacostal cells at the extreme base weakly porose); basal cells long rectangular, 60-100 um long, cells at the margins narrower, and thinner but not hyaline or forming a distinct limbidium; alar cells red-brown, well-developed, extending to the costa. Brood leaves commonly present in masses in the leaf axils at the stem apex. Sporophyte not seen.

Illustrations. Herzog (1916, Pl. 1 13, as C. trichophorus); Frahm (1978, Pl. 28, as C. trichophorus); Frahm (1991a, Fig. 34).

Habitat. On the upper branches of trees, trunks and terrestrial; 80-3130 m. Distribution in Central America. BELIZE. Belize: Davids & Brant 32958 (MO). COSTA RICA. Alajuela: Valerio 282 (US); Cartago: Croat 36095 (MO); Heredia: Crosby & Crosby 6559 (MO); Puntarenas: Crosby 9982 (MO); San Jose: Crosby 9762 (MO). PANAMA. Bocas del Toro: Allen 5740 (MO); Chiriqui: Croat 66498 (MO).

World range: Central America; Western and Northern South America.
Campylopus asperifolius is best recognized by its clusters of brood leaves borne on long stalks in the leaf axils at the stem apex. Campylopus fragilis has sessile brood leaves, lax, thin-walled, bulging basal cells and undifferentiated alar cells. When brood leaves are absent, C. asperifolius may be confused with C. densicoma or C. hoffmannii. The former has more subulate leaves with non-twisted, flexuous leaf apices. Both C. hoffmannii and C. asperifolius have distinctive penicillate-tipped stems, but in C. hoffmannii the leaves are long, subulate and spread from the base when dry.

7. Campylopus atlanticus Allen, Bryologist 93: 447. 1990. Type. Panama, Bocas del Toro, vicinity of Fortuna Dam, Allen 5713 (MO, holotype; PMA, isotype); paratype, Panama, Darien, Cerro Tacarcuna, Mori & Gentry 4492b (MO).

Plants medium to slender, yellowish green; stems 4-7 cm high, red, moderately tomentose, not comal tufted. Leaves 5-8 mm long, linear, flexuous-secund, slenderly setaceous; margins entire below to midleaf, serrate above, sharply and densely serrulate at the apex; costa excurrent, at base 1/3-1/2 the leaf width, dorsal surface smooth below, mammillose above, in cross section with ventral and dorsal stereid bands throughout the leaf, guide cells well-developed; basal juxtacostal cells 25-50 um | 7-10 um, enlarged, long-rectangular, firm-walled (occasionally a few cells porose), clearly differentiated from the small, quadrate to short rectangular (occasionally irregularly triangular), firm-walled, non-porous outer basal cells, 7-15 um | 7 um; basal marginal cells elongate but not forming a distinct border; median and upper leaf cells similar to the outer basal cells except for one or two rows of elongated intramarginal cells 12-20 um | 7 um; alar cells strongly differentiated in persistent, bulging, excavate groups that extend to the costa. Sporophyte unknown.
Illustrations. Allen (1990a, Figs. 1-10).

Habitat. Corticolous, on tree trunks; 1200-1860 m.

Distribution in Central America. HONDURAS. Cortes: Allen 14257 (MO).

PANAMA. Darien: Mori & Gentry 4429b (MO); Bocas del Toro: Allen 5713 (MO, PMA).

World range: Central America.

Campylopus atlanticus is nearly identical to C. anderssonii (C. Mull.) Jaeg., which differs in having enlarged ventral hyalocysts. It is similar to C. weberbaueri in its quadrate upper leaf cells, but C. weberbaueri is a more robust species (leaves 8-13 mm long) with strongly porose basal leaf cells and a comal-tufted habit. Bryohumbertia filifolia var. longifolia is similar in the form, cellular pattern, and marginal serrations of its leaves, but it is a more slender plant (leaves long setaceous to 15-20 mm long) and has a distinctive, comal-tufted habit.


Plants large, compactly tufted, greenish yellow, frequently dark reddish yellow, more or less glossy; stems moderately tomentose, to 8 cm long, hyalodermis present, of 1-2 layers of enlarged, thin-walled, hyaline cells. Leaves 10-12 mm long, stiffly erect, linear-lanceolate, apex setaceous; margins entire below, weakly toothed at the extreme apex; costa excurrent, at times subhyaline at tip, 3/4 the leaf width at base, dorsal surface smooth, in cross section ventral hyalocysts large and well developed, guide cells well developed, stereid cells present in the middle of leaf but not extending to costa margins, the edges of costa therefore composed of 2-3 layers of enlarged, thin-walled cells; upper cells narrowly oblong to linear, 20-50 μm long, incrassate, not porose, more or less flexuous; basal cells incrassate, not porose, long rectangular, near the costa 40-65 μm, becoming narrow and elongate toward the margins and forming a distinct border to 10 cells wide; alar cells reddish, weakly developed, frequently
remaining on stem when leaves are dissected away. Sporophytes not seen.

Illustrations. Frahm (1978, Pl. 5); Frahm (1991a, Fig. 41).
Habitat. Terrestrial, in shade of overhanging cliff; 3200–3350 m.

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World range: Central America; Western and Northern South America.

Campylopus cavifolius is a large plant with stiffly erect, setaceous leaves that in the lower half are distinctly bordered by to 10 rows of narrowly elongate cells. In cross section its costal dorsal stereid band is present only in the center, at the margins the costa is composed of 2-3 layers of enlarged, thin-walled cells. Campylopus areodictyon, the only Central American species likely to be confused with it, has shorter leaves (5-7 mm) and shorter (10-12 um), quadrate upper leaf cells.
Plants medium sized, green to yellowish green; stems lightly to moderately tomentose, 3-4 cm long. Leaves 8-11 mm long, erect-patent to erect-flexuous below, flexuous or stiffly spreading above above, lance-subulate, concave throughout, serrate in the upper 1/4; costa excurrent, concolorous, 1/2 the leaf width at base, smooth to lightly mammillose at back, in cross section with ventral hyalocysts larger than guide cells, dorsal stereids well developed; upper cells shortly rectangular, 10-17 um long, firm-walled; median cells rhomboidal, 15-35 um, firm-walled, not porose; basal cells long rectangular, 60-100 um long, firm-walled, cells near the costa porose or non-porose, those at the margins narrower, but not forming a hyaline border of narrow linear cells; alar cells red-brown in large bulging groups, extending to the costa. Setae 3-6 at apex of stem in comal tufts, 7-8 mm long, yellow-red; capsules erect to somewhat inclined, plicate when dry, 1.5 mm long, not strumose, but roughened at base; opercula 1.0 mm long. Calyptrae entire at base. Spores oval, 12-15 um.

Illustrations. Bartram (1928, Fig. 6 A-I, as C. straminifolius); Frahm (1978, Pl. 8; Pl. 11, as C. gertrudis); Frahm (1991a, Fig. 57).

Habitat. On bamboo, tree stumps and soil; 1050-3150 m.

Distribution in Central America. GUATEMALA. Chiquimula: Steyermark 30608 (F); Guatemala: Standley 80728 (F). HONDURAS. Comayagua: Allen 11036 (MO, TEFH); Cortes: Allen 14274 (MO, TEFH); Lempira: Allen 11931 (MO, TEFH); Ocotepeque: Allen 14533 (MO, TEFH); Olancho: Allen 12601 (MO, TEFH). COSTA RICA. Alajuela: Gomez 20014 (MO); Cartago: Standley & Torres 51212 (NY, US); Guanacaste: Hammel 17648A (MO); Heredia: Crosby & Crosby 6455 (MO); Puntarenas: Davidse et al. 23947 (MO); San Jose: Standley 43538a (FH, US). PANAMA. Bocas del Toro: Davidse et al. 25410 (MO).
World range: Central America; Western, Northern, and Southern South America, Brazil.

In Campylopus densicoma the well developed alar cells are distinctly bulging and the basal leaf cells near the costa are commonly porose, but, when all basal cells are non-porose (see, e.g., the type of C. straminifolius), this species may be confused with C. anderssonii, which has a similar habit. Campylopus anderssonii has quadrate median leaf cells and enlarged, bulging juxtacostal cells. Campylopus asperifolius is also similar, and both species have well-developed, distinctly bulging alar cells. But, C. asperifolius has shorter, stiffly erect leaf apices that are commonly twisted when dry. Although the basal marginal cells in C. densicoma can be long rectangular and somewhat border-like, they are never developed to the extent seen, for example, in C. nivalis or C. areodictyon.

Bartram (1949) and Frahm (1991a) placed C. straminifolius in the synonymy of C. flexuosus. However, C. flexuosus has a costa with ventral hyalocysts that are the same size or smaller than the guide cells. In C. straminifolius the ventral hyalocysts of the costa are enlarged.


   Plants small, tufted, yellow-green; stems variably tomentose, 1.5-2.0 cm long. Leaves 3-5 mm long, erect-patent, erect, or somewhat falcate-secund when wet, appressed to flexuous when dry, concave, lanceolate, apex acute to short acuminate; margins entire or a few teeth present at the extreme apex, not bordered by elongate cells; costa percurrent to shortly excurrent, 1/2-2/3 the leaf width, at times with low
mammillae, in cross section guide cells well developed, dorsal stereids present, ventral hyalocysts present but smaller than (at times equal to) the size of the guide cells; cells firm-walled, not porose; upper laminal cells subquadrate to short rectangular, 10-20 μm long; median cells irregularly rectangular; basal cells rectangular, usually firm-walled, at times with large lax, hyaline cells along the basal margins; alar cells differentiated, forming reddish brown to hyaline auricles. Brood bodies commonly in clusters at stem apex. Setae 4-7 mm long, red-yellow; capsules curved and asymmetrical, striate when dry, 1.5-2.3 mm long; peristome teeth dark red below, hyaline above, dorsal lamellae with prominent vertical bars below, papillose above, ventral lamellae papillose, teeth split 1/3-2/3 their lengths; opercula shortly rostrate, 1.0 mm long. Calyptrae cucullate 1.5-2.0 mm long, ciliate at base. Spores 10-15 μm.

Illustrations. Bartram (1929, Pl. 17 A-J, as Campylopus hondurensis); Bartram (1949, Fig. 19 A-D); Crum and Anderson (1981, Fig. 99 H-K); Frahm (1991a, Fig. 61).

Habitat. On decomposing logs and tree trunks; 1000-3333 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: Croat 41764A (MO); Guatemala: Standley 58424 (F); Jalapa: Steyermark 32489 (F); Quezaltenango: Sharp 2073 (MO); Quiche: Sharp 2525 (US); Totonicapan: Standley 62664 (F). EL SALVADOR. Santa Ana: Watson 35 (MO). HONDURAS. Comayagua: Allen 11050 (MO, TEFH); Lempira: Allen 11242 (MO, TEFH); Morazan: Standley 13726 (F);
Ocotepeque: Allen 14495 (MO, TEFH); Olancho: Allen 12752 (MO, TEFH); Santa Barbara: Allen 11707 (MO, TEFH). COSTA RICA. Cartago: Crosby & Crosby 6356 (MO); Heredia: Hatheway & Hatheway 1715 (US); Puntarenas: Davidse et al. 25695 (MO). PANAMA. Chiriqui: Davidse & D'Arcy 10329E (MO).

World range: Western Canada, Southeastern U.S.A.; Mexico; Central America; Caribbean, Western and Northern South America; Northern, Southwestern, Middle, East, and Southeastern Europe; Caucasus, China, Eastern Asia; Macaronesia, Northern Africa, Northeast, West-Central, East, and South Tropical Africa, Western Indian Ocean; Australia, New Zealand.

The combination of tumid brood bodies at the stem apex and costal ventral hyalocysts that are smaller or nearly as large as the guide cells distinguish this species. Campylopus savannarum also has apical brood bodies and although it lacks ventral hyalocysts, it has enlarged ventral stereid cells that form pseudo-hyalocysts. Campylopus savannarum is recognized by its numerous thick-walled, quadrate basal leaf cells, and its spurred, mammillose costa.

This species belongs to a complex of species that have small-sized ventral hyalocysts. In C. flexuosus the alar cells are distinctly differentiated, while in the other three species the alar cells are poorly or not differentiated.


Plants small, tufted, green to yellow-green; stems usually densely tomentose, 0.6-3.5 cm long. Leaves 3-5 mm long, erect-patent, more or less flexuous above when dry, lanceolate, oblong below, subulate above, serrulate toward the apex; costa ending at the apex, in cross section 2/3 the leaf width, lightly ribbed at back, guide cells well developed, dorsal stereids present, ventral hyalocysts present and larger than the guide cells, at base the dorsal stereid band not as wide as the costa, the margins of the costa therefore of 2-3 layers of enlarged hyaline cells; upper cells rhombodial; basal cells rectangular, hyaline, thin-walled, bulging, in dried material frequently remaining full of air on wetting, marginal basal cells narrower but not forming a distinct border, cells
Brood bodies minute, slender, at times clustered at the stem tips. Setae 5-8 mm long, reddish yellow; capsules erect to slightly curved when dry, 1.0-1.2 mm long; opercula shortly rostrate, 0.5 mm long. Calyptrae 1.0-1.2 mm long, fringed at base.

Illustrations. Grout (1937, Pl. 48 B); Bartram (1949, Fig. 19 E-F); Frahm (1978, Pl. 10); Smith (1978, Fig. 74 1-4); Frahm (1991a, Fig. 64).

Habitat. On humus, rotting logs and soil; 2500-3130 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: Croat 41757 (MO); Chimaltenango: Standley 58745a (FH); Huehuetenango: Sharp 4939a (FH); Quezaltenango: Sharp 1995 (FH); Quiche: Sharp 2484 (MO, NY, US); San Marcos: Croat 40918 (MO); Totonicapan: Standley 84107 (F). HONDURAS. Comayagua: Allen 12310 (MO, TEFH); Lempira: Allen 11238 (MO, TEFH); Morazan: Standley & Williams 428 (F); Olancho: Allen 12765 (MO, TEFH); Yoro: Allen 13557 (MO, TEFH). COSTA RICA. Alajuela: Brenes 17113 (F); Guanacaste: Brenes s.n. (FH); San Jose: Crosby & Crosby 6128 (MO).

World range: Western Canada, Southeastern U.S.A.; Mexico; Central America; Caribbean, Western and Northern South America; Northern, Southwestern, Middle, and Southeastern Europe; Soviet Far East, China, Eastern Asia,; Indian Subcontinent; Macaronesia, Northeast Tropical, West-Central Tropical, East Tropical, South Tropical, and Southern Africa.

Campylopus fragilis has enlarged hyaline cells throughout the leaf base, undifferentiated alar cells, and at times brood leaves clustered at the stem apices. The brood leaves in C. fragilis are identical to those found in Brothera leana (Sull.) C. Mull. Indeed, Bartram (1949) and Frahm (1991a) reported B. leana from Central America on the basis of small collections of C. fragilis that consist almost entirely of brood leaves. In B. leana the costa has a ventral and dorsal layer of hyalocysts, a median layer of stereid cells, and the upper leaf cells are long rectangular. Campylopus asperifolius has brood leaves borne on stalks, larger leaves, and firm-walled basal cells.

Campylopus tallulensis differs in having the costa in cross section with stereid bands extending to the margin, a more well-developed area of hyaline basal cells that continue
up the margins of the leaves forming a V-shaped pattern, and better, although still weakly, developed alar cells. In C. fragilis the costal stereid bands do not reach the margins of the costa, which consists of 2-3 layers of enlarged, thin-walled, hyaline cells, the inner and outer hyaline basal cells end at about the same level in the leaf, and the alar cells are undifferentiated.

   Type. Peru, Hasskarl s.n.

Plants medium, greenish yellow, growing in dense mats; stems moderately to densely tomentose, 3 cm long (to 8 cm long), simple to sparingly branched. Leaves laxly imbricate to erect-spreading above, flexuous-spreading below, concave when wet, at times appearing flattened below when dry, lanceolate-subulate, 5-8 mm long, moderately dentate or spinose dentate above; costa shortly excurrent, concolorous, 1/2-

2/3 the leaf width at base, smooth at back, in cross section guide cells well-developed, large ventral hyalocysts present, stereid band well-developed, in the lower 1/3 of leaf, not as wide as costa, margins of costa with 2-3 layers of enlarged cells; upper, median, and basal cells quadrate, 5-12 μm; lower basal cells rectangular, 35-40 μm long, at the margins a few rows extending upwards forming a V-shape pattern; alar cells well-developed, red-brown extending to the costa and frequently in excavate groups. Setae 6-7 mm long, red; capsules curved, furrowed when dry, 1.5-2.0 mm long; opercula conic-subulate, 1.0-1.2 mm long. Calyptrae cucullate, smooth at base. Spores not seen.

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12. Campylopus heterostachys

Illustrations. Frahm (1978, Pl. 12); Frahm (1991a, Fig. 75).

Habitat. On bark of trees, rotting logs, and terrestrial; 1050-2600 m.

Distribution in Central America. GUATEMALA. Huehuetenango: Sharp 4808 (MO, US); Quezaltenango: Standley 85675 (F, NY); San Marcos: Standley 86229 (F, FH); Zacapa: Steyermark 42660 (F). HONDURAS. Comayagua: Allen 12316 (MO, TEFH); Lempira: Allen 11238 (MO, TEFH); Morazan: Standley 12357 (F); Olancho: Allen 12452 (MO, TEFH). COSTA RICA. Alajuela: Standley & Torres 47460 (US); Cartago: Standley 39703 (US); Heredia: Croat 35542b (FH); San Jose: Griffin & Morales B95 (F). PANAMA. Chiriqui: Allen 5220 (MO).

World range: Mexico; Central America; Western, Northern, and Southern South America, Brazil.

The leaves of Campylopus heterostachys have relatively lax basal cells and a tendency for the basal marginal cells to form an indistinct border. This species has remarkably dimorphic leaves: the basal leaves are small and linear and have very reduced laminae, while the upper leaves are typical in form. A critical feature of C. heterostachys is found in its costa, where the stereid band in the lower 1/3 of the leaf does not reach the edge of the costa. In cross section the margins of the costa consist of 2-3 layers of enlarged thin-walled cells. Most collections of C. heterostachys from Central America have been called C. hellerianus (Hampe) Jaeg. and treated as a synonym of C. flexuosus. All Central American collections of C. concolor (Hook.) Brid. have here been referred to C. heterostachys, despite the fact that a few do not fit comfortably in the latter species. The two species have been separated by differences in
their basal leaf cells: C. heterostachys - thin-walled; C. concolor - thick-walled (see Frahm 1991a). This distinction appears unreliable, since it is possible to find a series of leaves from a single plant that will show both types of cells.

Campylopus anderssonii is close to this species in leaf form and in having lower basal cells that are similarly enlarged. In C. anderssonii the leaves are not flattened at the base when dry, the dorsal stereid band extends to the edge of the costa, and the inner basal leaf cells may at times be weakly porose. It may be that Central American collections of these taxa represent the same species.


Plants large, slender, yellow-green; stems moderately tomentose, to 17 cm long. Leaves 8-14 mm long, widely spaced, erect-spreading below, penicillate at apex, when wet spreading from an ovate base, long, slenderly setaceous above, concave throughout, serrate above; costa 1/3 the leaf width at base, frequently with short lateral spurs, shortly excurrent, concolorous, smooth to lightly ribbed on back, in cross section with well developed guide cells, ventral hyalocysts present, 1.5 times the size of the guide cells, dorsal stereid band well-developed; upper cells long rectangular, 12-25 um long, firm-walled; basal cells incrassate and porose, long rhomboidal to linear, those at the margins narrower and shorter but not forming a distinct border; alar cells well developed, red-brown in large, excavate groups extending to the costa, firm-walled. Setae 8-9 mm long, strongly geniculate both wet and dry; capsules ovoid-cylindric, 2 mm long, symmetrical, strongly furrowed when dry; opercula 1 mm long, conic-rostrate. Calyptrae not seen.


World range: Mexico; Central America.

This is a distinctive species that can be field-recognized by its large size, penicillate stem apices, and long, slender, distantly spaced leaves. Campylopus subcuspidatus and C. standleyi also are large plants with strongly porose leaf cells, but C. hoffmannii differs from those species by its leaves that are concave at base when dry, much narrower costa with short lateral spurs, and small costal ventral hyalocysts. Frahm (1978, 1991a) placed C. hoffmannii in the synonymy of C. cuspidatus, but the type of that species has entire, broadly lanceolate leaves 5-6 mm long with acuminate apices ending in hyaline points and linear upper leaf cells. In C. hoffmannii the leaves are linear-lanceolate, serrate above, 8-14 mm long with concolorous, setaceous apices and long rhombodial upper leaf cells.


Plants robust, greenish yellow, growing in dense mats; stems moderately to densely tomentose, to 12 cm long, simple to sparingly branched. Leaves spreading below, erect-spreading above, concave when wet, flattened when dry, lanceolate-setaceous, to 20 mm long, serrate in upper 1/4-1/2; costa excurrent, concolorous, to 4/5 the leaf width at base, smooth to lightly mammillose, in cross section guide cells well-developed, large ventral hyalocysts present, dorsal stereids well-developed; apical cells quadrate; median cells firm-walled, quadrate; basal cells near costa enlarged, firm-walled, not porose, elongate, those toward the margins smaller, firm-walled quadrate to
rectangular, those at the margin narrower but not forming a distinct border, cells just above the alar cells enlarged, lax, square to short rectangular, frequently bulging; alar cells well-developed in large groups extending to the costa and frequently excavate. Sporophyte not seen.

Illustrations. Hooker (1837, Pl. 179 1-9); Hegewald and Hegewald (1977, Figs. 9-14); Frahm (1978, Pl. 14); Frahm (1979, p. 176); Frahm (1985, Fig. 50); Frahm (1991a, Fig. 80). Habitat. Terrestrial, on shady road banks; 1500-3220 m.

Distribution in Central America. HONDURAS. Lempira: Allen 11592 (MO, TEFH). COSTA RICA. San Jose: Croat 32887b (MO).

World range: Mexico; Central America; Western and Northern South America, Brazil; West-Central Tropical, East Tropical, South Tropical and Southern Africa, West Indian Ocean.

This robust moss is likely to be confused only with Campylopus standleyi or C. subcuspidatus. Typically C. standleyi has leaves less than 15 mm long, porose
juxtacostal basal cells, rectangular, firm-walled and not particularly enlarged basal cells above the alar cells, linear marginal basal cells, and leaves serrulate only at the extreme apex. Some collections of C. standleyi closely approach C. jamesonii (see discussion under C. standleyi). Campylopus subcuspidatus has strongly porose leaf cells, leaves serrulate only at the extreme apex, and a short basal border of hyaline, linear cells.

   Colombia, Bogota, Cipacon, Lindig.

   Plants medium, forming dense greenish yellow tufts; stems tomentose at base, to 3.0 cm long, unbranched or with single branches occurring beneath comal tufts. Leaves flexuous at base, becoming abruptly appressed to the stem, then crowded and spreading in apical comal tufts, branch leaves appressed, leaves exceedingly variable in shape: basal leaves small, 3-4 mm long, ovate-lanceolate, appressed leaves and comal leaves 5-6 mm long, oblong-lanceolate, comal tuft leaves long-subulate; all leaf margins concave below, tubulose above, not bordered by elongated cells, weakly serrate at apex, usually entire below; costa percurrent in basal leaves, percurrent or variably excurrent in other leaves, smooth at back (at times weakly roughened), in cross section with ventral hyalocysts equal to or smaller than the guide cells, dorsal stereid band well-developed; upper cells rhombic; median cells rhomboidal, incrassate and smooth walled; basal cells variable: those of the basal leaves short rectangular, firm-walled, in other leaves long rectangular variably firm- or lax-walled; alar cells moderately developed, red-brown, not conspicuously bulging beyond the leaf margin. Sporophytes unknown in Central America.

Illustrations. Frahm (1978, Pl. 15).
Habitat. Rotting tree fern; 2680 m.
World range: Mexico; Central America; Western and Northern South America.

The presence of costal ventral hyalocysts that are equal in size or smaller than the guide cells is an important feature that links Campylopus lamprodictyon and C. surinamensis. In Central America the only features that will consistently separate the two species are the smooth costa and the weakly serrate leaf margins of C. lamprodictyon. Campylopus surinamensis has strongly dentate leaf apices, the comal leaves may be hyaline tipped and the costa is mammillose at the back.


Plants slender to medium sized, tufted, pale yellow-green, usually glaucous; stems 10 cm long, epidermis of enlarged thin-walled cells. Leaves crowded, lanceolate, when dry erect-spreading, concave, 5-8 mm long, apex narrowly acuminate to subulate; margins incurved above, entire below, denticulate at the extreme apex; costa long excurrent, 5/8 of the leaf width at base, dorsal surface roughened, in cross section the ventral hyalocysts well developed, guide cells poorly developed, dorsal stereid cells absent or pseudostereids present in middle of costa and not reaching the ends, which consist of 2-3 layers of enlarged, thin walled cells; upper cells oblong-rectangular to hexagonal, 14-22 um long, walls thickened, not porose, basal cells laxly rectangular, those near the costa enlarged, hyaline, thin-walled and bulging, those at the margins linear, forming a distinct hyaline border; alar cells weakly differentiated, frequently fugacious, red-brown, thin-walled. Setae 7-15 mm long, red-brown, roughened above; capsules erect, cylindrical, 1.5-2.0 mm long, furrowed when dry, red-brown,
roughened at base; opercula rostrate, 1.0-1.3 mm long. Calyptrae cucullate, 2.5 mm long, entire at base.

Illustrations. Bartram (1949, Fig. 18 F-J, as C. chrismarii); Frahm (1978, Pl. 6, as C. chrismarii, Pl. 26, as C. suboblongus); Frahm (1980a, Fig. 13, as C. chrismarii); Frahm (1985, Figs. 63-64); Frahm (1991a, Fig. 93).

Habitat. On soil, fallen logs, tree trunks and branches in open pastures or shaded, wet forests; 1800-4400 m.

Distribution in Central America. GUATEMALA. Chimaltenango: Standley 61847 (F); Huehuetenango: Sharp 4945 (F); Quezaltenango: Steyermark 34182 (F, NY); Quiche: Standley 62461 (FH); San Marcos: Steyermark 36104 (F); Tontonicapan: Standley 62688 (F). HONDURAS. Comayagua: Allen 11009 (MO, TEFH); Cortes: Allen 14247 (MO); Lempira: Allen 12294 (MO, TEFH); Santa Barbara: Allen 11673 (MO, TEFH). COSTA RICA. Alajuela: Griffin & Araya 47 (F, MO, NY); Cartago:
16. Campylopus nivalis  
Crosby 9787 (MO); Puntarenas: Hammel et al. 15081 (MO); San Jose: Crosby 3905 (MO). PANAMA. Bocas del Toro: Davidse et al. 25298A (MO); Chiriqui: Allen 9142 (MO). World range: Mexico; Central America; Caribbean, Western, Northern, and Southern South America, Brazil; West, East, and South Tropical Africa, Southern Africa, Western Indian Ocean.

   Campylopus nivalis, long known as C. chrismarii, usually has a glaucous color, narrow, erect-spreading leaves, a well defined basal leaf border, lax basal cells, and broad costa (to 5/8 the leaf width at base) with dorsal pseudostereids. There is a puzzling dark green expression of the species that grows on soil and is marked by short, fragile stems and narrow, frequently deciduous leaves. This expression has the typical costal cross section and basal leaf cells of C. nivalis.

   Campylopus aerodictyon and C. albidovirens also have costae with pseudostereids or no stereid development. In C. aerodictyon, the plants are shiny yellowish green, the leaves are stiffly erect, and the leaf cells are shorter (5-12 um long). Campylopus albidovirens lacks stereid development in the costa, has shorter, broader leaves, a weakly developed leaf limbidium, and smaller, more firm-walled inner basal cells. The calyptrae are entire in C. nivalis but fringed in C. albidovirens.

17. Campylopus oerstedianus  


   Plants small, densely tufted, yellowish green above, brownish below; stems densely red-tomentose below, to 1.0 cm high. Leaves erect-appressed, subtubulose above, occasionally tightly appressed on stems and comal tufted above, 2-4 mm long, oblong-lanceolate and gradually narrowed to a moderately long subula, usually ending in a short, hyaline tip, the perichaetial leaves ending in a long serrate awn; margins above the shoulders narrowly incurved, sharply serrulate; costa percurrent to short-excurrent
(perichaetial leaves excurrent as an awn), in cross section with ventral hyalocysts equal to or smaller than the guide cells, dorsal stereid band well-developed; upper cells irregularly trapezoidal to short-rhomboidal, obliquely oriented, basal cells enlarged, long-rectangular becoming abruptly short-rectangular to nearly quadrate, typically firm-walled, occasionally thin-walled; alar cells weakly differentiated, reddish or hyaline in slightly auriculate groups. Sporophyte unknown.

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18. Campylopus paramoensis

19. Campylopus pilifer

Illustrations. Frahm (1975, Fig. 14); Frahm (1980, Figs. 4-9); Crum and Anderson (1981, Fig. 99 L-O); Frahm (1991a, Figs. 99-100).

Habitat. On tree; 3750 m.

Distribution in Central America. HONDURAS. Yoro: Allen 13532 (MO, TEFH).

COSTA RICA. Cartago: Oersted s.n. (NY).

World range: Southeastern U.S.A.; Central America; Caribbean; Southwestern and Southeastern Europe.
Campylopus oerstedianus, along with C. surinamensis, C. lamprodictyon, C. pauper, and C. pilifer, is characterized by small ventral hyalocysts and a tendency toward a comal-tuft morphology. It has the same leaf shape and areolation as C. surinamensis, which is a larger plant, with a better developed comal-tuft morphology, and only hyaline tipped perichaetial leaves. From C. pilifer it differs by its lack of costal lamellae. The comal-tuft morphology is weakly developed in C. oerstedianus, but its presence is also erratic in other members of the group.


Plants slender to medium in compact tufts, reddish yellow above, blackish below; stems reddish, radiculose, to 3 cm long. Leaves evenly spaced, erect-spread when wet, stiffly erect-appressed when dry, strongly concave to tubulose, lanceolate-subulate, 3-7 mm long; margins entire below, denticulate at apex, marginal cells elongate but not forming a distinct border; costa 2/3 the leaf width at base, excurrent as a hyaline hair-point, smooth at back, in cross section ventral hyalocysts large, well developed; guide cells and dorsal stereids well developed; upper cells linear-flexuous to linear, 35 um | 3-5 um, incrassate, end walls rounded, basal cells short rectangular to rhomboidal, incrassate, porose; alar cells forming distinct groups of reddish to hyaline, thin-walled cells. Sporophytes unknown.

Illustrations. Bartram (1928, Fig. 4 A-F, as C. atratus).
Habitat. On wet bank; 2700-3000 m.
World range: Central America.

This species is distinguished by hyaline hair-pointed leaves, incrassate leaf cells that
are linear-flexuous above and porose at base, and enlarged, ventral, costal hyalocysts. It superficially resembles Campylopus richardii, but that species has ventral stereid cells in the costa and obliquely rhomboidal upper leaf cells. Frahm (1991a) treated C. paramoensis as a synonym of C. subcuspidatus, but that species is a more robust plant that lacks hyaline tipped leaves and has a hyaline basal leaf limbidium.


Plants small to medium, tufted, yellow-green to brownish yellow; stems variable in length, 1.0-6.5 cm long. Leaves crowded, erect-spreading when wet, appressed when dry, oblong-lanceolate, 3-6 mm long, subulate at apex and ending in a long, toothed, hyaline hair-point, to 1.9 mm long; margins subtubulose above, entire below, denticulate at apex; costa excurrent, dorsal surface with 2-6 cell high lamellae in the upper 2/3 of the leaf, in cross section with ventral hyalocysts either smaller than or distinctly larger than the guide cells, dorsal stereids well developed; upper cells oval to oblong, incrassate, not pitted, basal cells elongate-rectangular, bulging, hyaline, thin-walled; alar cells more or less quadrate in small weakly differentiated, reddish yellow groups. Setae 4-8 mm long, red-yellow, frequently aggregate from comal tufts, roughened above, smooth below; capsules erect, symmetric, cylindrical-ellipsoid, 1.0-1.5 mm long, scabrose at base, red-black; opercula short rostrate to long conic, 0.5-1.0 mm long. Calyptrae cucullate, 1.5-2.0 mm long, ciliate at base.

Illustrations. Bartram (1949, Fig. 20 F-I, as C. introflexus); Frahm (1974, Fig. 6, as C. polytrichoides); Hegewald and Hegewald (1974, Figs. 1-4); Frahm (1978, Pl. 19); Frahm (1979, p. 177); Crum and Anderson (1981, Fig. 96); Frahm (1985, Fig. 73); Frahm (1991a, Figs. 105-106).

Habitat. On soil, along roadsides and in forest, bare rock, lava, occasionally on logs and trees; 300-3500 m.

Distribution in Central America. BELIZE. Cayo: Mains 4068 (F, US); Toledo: Davidse & Brant 32180 (MO); GUATEMALA. Alta Verapaz: Turkheim (NY); Baja Verapaz: Sharp 2668 (US); Chimaltenango: Kellerman s.n. (US); Escuintla: Eglger 523 (NY); Guatemala: Standley 80732 (F); Huehuetenango: Standley 82308 (F, NY); Jalapa: Steyermark 32602 (F, NY); Jutiapa: Standley 75594 (F); Quezaltenango: Standley 84735 (F, NY); Quiche: Sharp 2538 (US); Sacatepequez: Standley 58816 (F); San Marcos: Standley 68535 (F); Solola: Hermann 26339 (F, NY); Totonicapan:
Standley 84103 (NY). EL SALVADOR. Chalatenango: Winkler 20 (MO); San Miguel: Eggler 701 (NY); Santa Ana: Winkler 29 (MO); Sonsonate: Eggler 705 (NY).
HONDURAS. Comayagua: Allen 12315 (MO, TEFH); Cortes: Allen 14054 (MO, TEFH); El Paraiso: Standley 14867 (F); Lempira: Allen 13376 (MO, TEFH); Morazan: Allen 12345 (MO, TEFH); Olancho: Allen 12489 (MO, TEFH).
NICARAGUA. Jinotega: Croat 43028 (MO); Managua: Stevens 4547 (MO); Masaya: Stevens 5289 (MO); Matagalpa: Guzman & Castro 1623c (MO). COSTA RICA. Alajuela: Crosby 3615 (MO); Cartago: Alfaro 118 (F, US); Heredia: Croat 35539A (MO); Puntarenas: Crosby 2486 (MO); San Jose: Crosby 9759 (MO). PANAMA. Chiriqui: Crosby 4006 (MO); Panama: Crosby 4355 (MO).

World range: Southwestern, South-Central and Southeastern U.S.A.; Mexico; Central America; Caribbean, Western, Northern, and Southern South America, Brazil; Northern, Southwestern, Middle and Southeastern Europe; Indian Subcontinent; Macaronesia, Northern Africa, West-Central, East, and South Tropical Africa, Southern Africa, Western Indian Ocean.

Campylopus pilifer has 2-6 cell high lamellae on the back of the costa, long, hyaline, serrate, leaf hair-points, and enlarged, hyaline, thin-walled basal leaf cells.

Although dorsal lamellae are always present on the costa, their height and number are variable. There are two distinct expressions of C. pilifer in Central America. One has plants with comal tufts at the ends of long erect stems bearing rigidly appressed leaves, and leaves with costal ventral hyalocysts smaller than the guide cells (e.g., Allen 14054, MO). The other lacks comal tufts, has leaves stiffly erect with incurved apices, and costal ventral hyalocysts distinctly larger than the guide cells (e.g., Allen 11281, MO). These two expressions most likely represent two species. The comal tufted form belongs to the subgroup of Campylopus characterized by small costal ventral hyalocysts and a comal tufted morphology.


Plants medium to robust, yellowish green at tips, dark brown to black below; stems 3-6 cm long. Leaves on fertile stems appressed below, in comal tufts above, oblong-lanceolate, 3-8 mm long, apex acute, hyaline hair-pointed; margins concave below, tubulose above, entire; costa excurrent, mammillose at back, in cross section with small guide cells, dorsal stereid cells well-developed, ventral stereid cells weakly developed, consisting of only a single layer or absent, if absent guide cells ventrally exposed; upper cells obliquely rhomboidal; basal cells linear-rectangular, all incrassate-pitted; alar cells forming distinct groups of red-yellow cells. Setae 4-8 mm long, red-black, rough above; capsules erect, symmetric, cylindrical-ellipsoid, 1.5-2.0 mm long, scabrous at base, red-black; opercula rostrate, 1 mm long. Calyptrae 2 mm long, ciliate at base.

Illustrations. Bartram (1949, Fig. 22 D-H); Frahm (1978, Pl. 21); Frahm (1979, p. 177); Frahm and Gradstein (1987, Pl. 1 d); Frahm (1991a, Fig. 113).

Habitat. On gravel and soil, road banks and exposed rocks; 900-3447 m.

Distribution in Central America. GUATEMALA. Chimaltenango: Standley 61676
World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

Campylopus richardii is recognized by its leaves with hyaline hair-tips, short, incrasate, porose leaf cells, and the frequent absence of costal ventral stereid cells. When ventral stereids are absent the ventrally exposed costal guide cells can be mistaken for hyalocysts. Previously excluded from Guatemala (Allen 1989), the species has since been confirmed for that country. It may be confused with C. pilifer, C. paramoensis, C. valerioi, or the hair-tipped expression of C. savannarum. The first two have ventral hyalocysts in their costae. Campylopus savannarum has non-porose leaf cells and quadrate basal cells. Campylopus valerioi is a larger plant with leaves at base having a short hyaline border of elongate cells.


Plants medium, tufted, yellow-green; stems densely tomentose, to 6 cm long. Leaves evenly spaced, crowded, erect-spaying when wet, erect-appressed to more or less flexuous when dry, concave, linear-lanceolate to lanceolate, 2.5-7.0 mm long, apex acute or acuminate, at times hyaline awned; margins inflexed above, serrate in upper 1/4; costa long- to short-excurrent, excurrent part serrate and at times hyaline, frequently spurred, dorsal surface strongly mammillose, in cross section guide cells
well developed, ventral and dorsal stereids present; upper cells variable, elongate-rhomboidal to rhomboidal to oval, incrassate not pitted, basal cells quadrate to transversely elongate above alar cells, incrassate, not pitted; alar cells variable, usually strongly differentiated, red-brown or hyaline. Brood bodies at times clustered along the stems. Sporophytes unknown in Central America.

Illustrations. Bartram (1932, Fig. 1 A-G, as C. bartlettii); Bartram (1949, Fig. 21 A-F); Florschutz (1964, Fig. 23); Frahm (1979, p. 177); Frahm (1991a, Figs. 115, 116).

Habitat. On branches in crowns of shrubs and at base of trees, rocks, and soil of road banks; 1000-1500 m.

Distribution in Central America. BELIZE. Cayo: Bartlett 12973 (F, MO, NY). GUATEMALA. Baja Verapaz: Sharp s.n. (US); Chiquimula: Steyermark 30599 (F); Quezaltenango: Steyermark 33672 (F); San Marcos: Steyermark 37135 (F); Suchitepequez: s. coll. (FH); Totonacapan: Standley 84103 (F). HONDURAS. Comayagua: Allen 10977 (MO, TEFH); Intibuca: Allen 11093 (MO, TEFH); Lempira: Allen 11858 (MO, TEFH); Morazan: Standley 12360 (F); Olancho: Allen 12476 (MO, TEFH). NICARAGUA. Esteli: Stevens 10367 (MO); Jinotega: Standley 10353 (F); Matagalpa: Guzman & Castro 1623A (MO); Nueva Segovia: Stevens 3327 (MO); COSTA RICA. Alajuela: Brenes 109 (F); Heredia: Svihla 3059 (FH); Puntarenas: Crosby 2620 (MO); San Jose: James s.n. (US). PANAMA. Bocas del Toro: Allen 5167 (MO); Chiriqui: Allen 4999 (MO); Darien: Allen 8925 (MO); Panama: Crosby 4454 (F, MO, NY).

World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

Campylopus savannarum is a distinctive species marked by its broad leaves having many quadrate to shortly rectangular (frequently oblate) cells just above the alar region
and a spurred, strongly mammillose costa. Campylopus arctocarpus differs in having elongate, porose leaf cells above the alar region and costae that are neither spurred nor mammillose at back. Short, tumid brood bodies are sometimes found along the stems in both species. At times C. savannarum appears to have small, poorly developed ventral hyalocysts. These collections key to C. flexuosus, but that species lacks quadrate basal cells, narrower leaves, and unspurred costa. Campylopus bartlettii represents a robust expression of C. savannarum with pronounced excurrent, hyaline costa, and long upper leaf cells.


Plants robust, yellowish green; stems moderately to densely tomentose, to 15 cm long. Leaves flexuous when dry, lanceolate-subulate, gradually narrowed to a long, filiform point from an ovate-oblong base, lamina extending nearly to the apex, serrulate above; costa shortly excurrent, concolorous, to 4/5 the leaf width at base, smooth to
lightly mammillose at back, in cross section guide cells well-developed, large ventral hyalocysts present, dorsal stereids well-developed; upper cells oval, incrassate, not porose; median cells oblong to oval, incrassate and porose near the costa; basal cells near costa elongate-rectangular, firm-walled, more or less porose, becoming shorter toward the margins, those at the margins elongate and narrow; alar cells well-developed, extending to the costa in large dark red groups, not greatly bulging. Setae 12-14 mm long, smooth; capsules curved, furrowed when dry, more or less strümosse, 2 mm long; opercula 1.5 mm long, conic-rostrate, oblique. Calyptrae 2 mm long, entire at base.

Illustrations. Bartram (1928, Fig. 2 A-J): Bartram (1949, Fig. 20).

Habitat. Terrestrial, rotting wood and tree trunks; 1050-3700 m.

Distribution in Central America. GUATEMALA. Huehuetenango: Steyermark 50188a (F, FH). HONDURAS. Lempira: Allen 11432 (MO, TEFH). COSTA RICA. Cartago: Crosby & Crosby 8592 (MO); Puntarenas: Davidson 24350a (MO); San Jose: Crosby 10886 (MO). PANAMA. Bocas del Toro: Davidse et al. 25298 (MO); Chiriqui: D'Arcy et al. 12560A (MO).

World range: Central America.

Campylopus standleyi is a robust species with leaves having a broad costa (to 4/5 the leaf width), weakly porose basal cells, oblong to oval upper cells, an indistinct basal limbidium, and serrulate leaf apices. Frahm (1991a) treated the species as a synonym of C. jamesonii and distributed the collections here named C. standleyi between that species and C. subcuspidatus. Campylopus subcuspidatus has strongly porose cells in the lower half of the leaf, a distinct hyaline leaf border of narrow, elongate cells in the lower 1/4 to 1/2, and elongate upper leaf cells. Campylopus jamesonii has interior basal cells enlarged and firm-walled but not porose, median and upper leaf cells quadrate, and leaf margins serrate in the upper 1/2.

Most Central American material of C. standleyi clearly differs from C. jamesonii in its porose interior basal cells, leaves serrulate only at the apex, and firm-walled basal cells just above the alar cells. However, some collections (Koch 5090, NY, US and Croat 32885, MO) have porose basal cells but either quadrate median cells or leaf
margins serrate in the "jamesonii" manner. These collections are from a locality in which typical C. jamesonii is also found.


Plants robust in dense, yellowish green mats; stems densely tomentose, to 14 cm long. Leaves erect-patent to spreading-lanceolate, concave when wet, flattened when dry, narrowly acuminate, 8-15 mm long, denticulate at the apex, entire below; costa shortly excurrent, concolorous or at times hyaline at the extreme apex, to 4/5 the leaf width at base, smooth to lightly mammillose at back, in cross section guide cells well-developed, large ventral hyalocysts present, dorsal stereids well-developed; upper cells elongate-rhomboidal to linear, incrassate, not porose; median cells linear, incrassate, usually porose, those near the margins shorter; basal cells elongate, linear, incrassate and porose throughout, those at the basal margins narrower and elongate, not porose, forming a distinct hyaline border; alar cells well developed, red-brown, extending to the costa and frequently in excavate groups. Setae 15-20 mm long; capsules curved, furrowed when dry; opercula conic-rostrate, 1.0 mm long. Calyptrae entire at base.

Illustrations. Florschutz (1964, Fig. 19 A-I, as C. praealtus); Frahm and Gradstein (1987, Pl. 1 b); Frahm (1991a, Fig. 123).

Habitat. Terrestrial over rock; 884 m.

Distribution in Central America. BELIZE. Stann Creek: Stevenson 3 (F, FH).

World range: Central America; Caribbean, Northern South America, Brazil.

More commonly known in the Caribbean as Campylopus praealtus, this robust moss has porose leaf cells, a broad costa (to 4/5 the leaf width), elongate upper leaf cells,
and a distinct hyaline basal leaf limbidium. Campylopus jamesonii differs in its quadrate leaf cells, lack of porose leaf cells, and elimbate condition; C. standleyi lacks a leaf limbidium, has only the basal cells near the costa porose, and oval upper leaf cells. Campylopus paramoensis, another species with elongate upper leaf cells, is a smaller plant that has hyaline tipped leaves, and lacks a hyaline basal leaf limbidium.

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Plants medium sized, forming loose tufts, yellowish to bright green; stems variously tomentose, to 3.5 cm long. Leaves typically spreading at base, becoming abruptly
appressed to the stem, then crowded and spreading in apical comal tufts, exceedingly variable in shape: basal leaves oblong-ovate, acute, to 3 mm long, concave; margins inflexed, serrate at apex, not bordered by elongate cells; upper leaves linear-lanceolate, concave, acute, to 2-4 mm long, serrate or entire, not bordered by elongate cells; costa percurrent in basal leaves, excursive in others, at times more or less hyaline, ridged on back and dorsally serrate above, frequently spurred, in cross section with ventral hyalocysts equal to or smaller than the guide cells, dorsal stereids well developed; upper cells short to long rhomboidal, firm-walled not pitted, median cells rhomboidal to rectangular, firm-walled, basal cells above the alar cells quadrate to rectangular, thin walled; alar cells of basal leaves inflated, brown, well-developed, alar cells of other leaves poorly developed, hyaline. Perichaetial leaves frequently hyaline hair-tipped. Sporophytes unknown in Central America.

Illustrations. Bartram (1928, Fig. 5); Florschutz (1964, Fig. 22); Frahm (1978, Pl. 26); Frahm (1980, Fig. 10); Crum and Anderson (1981, Figs. 97 A-E, 98 G-K, 99 A-G); Frahm (1991a, Figs. 126-127).

Habitat. On tree and tree stumps; 25-800 m.


World range: Southeastern U.S.A.; Central America; Caribbean, Western and Northern America, Brazil.

In its typical form Campylopus surinamensis is recognized by its short basal rosette of spreading leaves that abruptly give way to an elongate stem with tightly appressed leaves crowned by a comal tuft of spreading leaves. Frequently the comal leaves are hyaline hair-pointed. The leaves on a single plant can be exceedingly variable. When keying plants, leaves from stems bearing appressed leaves should be examined. In these leaves the alar cells are poorly developed, the costa excursive, and the leaf margins distinctly serrate. Important microscopic features of this species include its thin-walled, non-porose basal leaf cells and ridged costa that in cross section has ventral hyalocysts usually smaller than the guide cells. This last feature separates C. surinamensis from all
other species except C. flexuosus, C. zygodonticarpus, C. oerstedianus, C. lamprodictyon, C. angustiretis, and C. pilifer.

Frahm's (1991a) report of this species from Honduras is based on a collection from "British Honduras" (= Belize).

25. Campylopus tallulensis Sull. & Lesq. ex Sull., Icon. Musc. 27. 1864. Type:

Plants medium sized, sordid green to yellow-green, growing in dense tufts; stems moderately to densely tomentose, to 3 cm long. Leaves erect to erect-spreading, moderately flexuous above, tubulose, ovate-lanceolate to lanceolate, broadly acuminate, the lamina distinct to the acute apex, 4-5 mm long, margins entire below, more or less toothed at the extreme apex; costa percurrent to shortly excurrent, 1/3-1/2 the leaf base, smooth to lightly ribbed at back, in cross section with ventral hyalocysts larger than the guide cells (at times only moderately larger), guide cells well-developed, stereid band well-developed, in the lower 1/3 of leaf the stereid band not as wide as the costa, the margins of the costa consisting of 2-3 layers of enlarged cells; upper cells shortly rectangular to quadrat, firm-walled; upper basal cells quadrat to rectangular, chlorophyllose, firm-walled; lower basal cells hyaline, short-rectangular, those nearest the costa largest, marginal cells thinner, and forming a narrow, hyaline border which extends upwards a short distance as a V-shaped border; alar cells poorly developed, frequently fugacious. Setae 8 mm long, red, twisted and erect when dry, strongly cygneous when wet; capsules 1.0-1.5 mm long, erect and striate when dry; opercula rostrate, 1.0 mm long. Calyptrae 2.0-2.5 mm long, cucullate, fringed at base.

Illustrations. Sullivant (1864, Pl. 17); Grout (1937, Pl. 50 A); Frahm (1978, Pl. 27); Crum and Anderson (1981, Figs. 100 C-I, 101 A-F); Frahm (1991a, Fig. 128).

Habitat. On soil, rocks and logs in forest; 300-3300 m.

Distribution in Central America. BELIZE. Cayo: Davidse & Brant 33056A (MO).
GUATEMALA. Guatemala: Standley 80620 (FH). HONDURAS. Comayagua: Crosby 2809 (MO); Morazan: Allen 12398 (MO, TEFH); Santa Barbara: Allen 11623 (MO,
Campylopus tallulensis has shortly acuminate, nearly entire leaves, a lamina that extends nearly to the apex, and lower basal leaf cells that are enlarged, hyaline, and continue up the margins in a distinctive V-pattern. The median leaf cells are quadrate, firm-walled, chlorophyllose and provide a strong contrast to the thin-walled, bulging, hyaline lower basal cells. Campylopus surinamensis and C. zygodonticarpus are similar but have firm-walled basal cells and small costal ventral hyalocysts. Campylopus heterostachys differs in its spinous-serrate leaves and well-developed alar cells. Campylopus fragilis has costal stereid bands that do not reach the margins of the costa, which consists of 2-3 layers of enlarged, thin-walled, hyaline cells. In addition, the enlarged hyaline basal cells grade more evenly into the quadrate median cells and asexual brood leaves are commonly present.
26. *Campylopus valerioi*  


Plants large, caespitose, pale green to yellow above, fulvous brown below; stems tomentose, comal tufted, to 10 cm long. Leaves 7–13 mm long, stem leaves erect, comal leaves flexuous-spreading, lanceolate, oblong below, long-subulate, serrate 1/4 or more above, upper leaves variously hyaline-tipped; costa percurrent to shortly excurrent, at base 1/3 the leaf width, sharply serrate above at back, in cross section the guide cells well developed, ventral hyalocysts absent, dorsal and ventral stereid bands well-developed; upper cells short, obliquely rhomboidal, 10–22 um long, firm-walled, weakly porose or smooth walled; basal cells long rectangular, 50–85 um long, strongly incrassate and porose, those at the basal margins long, narrow, hyaline, forming a short, distinct border; alar cells reddish brown in excavate groups. Setae clustered in comal tufts, cygneous, 5–7 mm long, red-black, smooth to roughened above; capsules erect, symmetric, cylindrical, 2.0 mm long, scabrous at base, red-black; annuli well developed; peristome teeth inserted below the mouth, linear, divided 2/3 their lengths, 0.40–0.65 mm long, red, papillose throughout, in obscure vertical rows at base; opercula erect, conic-rostrate, red, 1 mm long. Calyptrae 2–3 mm long, ciliate at base. Spores 10–12 um, lightly papillose, yellow.

Illustrations. Bartram (1929a, Fig. 1 A-K, as Dicranum costaricense).

Habitat. On tree trunks, soil and wet rocks; 1400–3100 m.

Distribution in Central America. COSTA RICA. Heredia: Stevens 13954 (MO); Limon: Davidse et al. 25909 (MO); Puntarenas: Crosby 9982 (MO); San Jose: Crosby & Crosby 6260 (MO). PANAMA. Bocas del Toro: Allen 5080 (MO); Chiriqui: Allen 9083 (MO).

World range: Central America.

Distinctive features of this moss include its robust, comal-tufted habitat, costa with
ventral stereids, hyaline-tipped leaves, strongly porose and incrassate leaf cells, well-
developed alar cells, and leaves bordered at base by a few rows of long, narrow, hyaline cells. This is the first report of sporophytes for the species.

Campylopus weberbaueri, which is similar in size and habit, has quadrate upper leaf cells. Bryohumbertia filifolia var. longifolia is structurally similar, but it is a much more slender plant with narrow, elimate leaves. Campylopus richardii differs in its smaller size, the near absence of a comal-tufted habit, elimate leaves, and non-excavate alar cells; the sporophytes of both species are identical.


Plants large, laxly caespitose, pale green to yellow; stems moderately red-
tomentose, with comal tufts, 2-6 cm long. Leaves 8-13 mm long, circinate above, stem leaves erect, comal leaves patent, narrowly lanceolate, oblong below, long-subulate above; margins serrate; costa percurrent to shortly excurrent, 1/3-1/2 the leaf width at base, sharply serrate above at back, in cross section guide cells well-developed, ventral hyalocysts absent, dorsal and ventral stereid bands well-developed; upper cells quadrate, firm-walled, not porose; basal cells long rectangular, incrassate and porose, those at the margin narrower, forming an indistinct, non-hyaline border; alar cells reddish brown, in excavate groups. Setae clustered in comal tufts, 7-8 mm long, yellow; capsules oval, inclined, plicate when dry, 1.5-2.0 mm long, strumose at base. Calyptrae ciliate at base.

Illustrations. Robinson (1967, Figs. 8-11, as Campylopus wurdackii); Frahm (1978, Pl. 30); Frahm (1991a, Fig. 77).

Habitat. Corticolus on upper tree branches; 1200 m.
Distribution in Central America. PANAMA. Bocas del Toro: Allen 5769 (MO).
World range: Central America; Western South America.

Campylopus weberbaueri is distinguished from all species in Group A by its robust size and quadrate upper leaf cells. Campylopus valerioi is similiar in size and habit, but it has rhomboidal upper leaf cells.


Plants small, tufted, green to yellow-green; stems variably tomentose, 1.0–3.0 cm long. Leaves 2.5–6.0 mm long, erect at base, flexuous above when dry, concave, lanceolate-subulate; apex long subulate; margins with a few teeth at the extreme apex or serrulate above, not bordered by elongated cells; costa shortly excurrent, 1/3–1/2 the leaf width, smooth or lightly ribbed at back, in cross section guide cells well developed, dorsal stereids present, ventral hyalocysts smaller than or a little larger than the guide cells; median and upper leaf cells quadrate to rectangular, thick-walled, not porose; basal leaf cells firm- or lax-walled, inner basal cells near costa enlarged, quadrate to shortly rectangular, contrasting strongly with the shorter, quadratic, outer basal cells; alar cells poorly developed, hyaline to light brown, frequently fugacious. Setae 7–10 mm long, deep red or yellow; capsules erect, striate when dry, 1.0–1.5 mm long; peristome teeth dark red below, hyaline above, dorsal lamellae with prominent vertical bars below, papillose above, ventral lamellae papillose, teeth split 1/3–2/3 their lengths; opercula shortly rostrate, 1.0 mm long. Calyptrae 1.5 mm long, variously fringed at base, at times fringed and unfringed in same collection.
28. Campylopus zygodonticarpus

Illustrations. Frahm (1978, Pl. 31); Crum and Anderson (1981, Fig. 98 A-F, as C. surinamensis "donnellii" expression); Frahm (1991a, Fig. 139).

Habitat. Tree trunks and branches, rotting logs, humus at base of stumps, wet soil banks and cliffs; 950-2650 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: Standley 90784 (F, NY); Baja Verapaz: Sharp 5191 (F); Quezaltenango: Standley 85913 (F, US); Quiche: Sharp 2535 (MO). EL SALVADOR. Santa Ana: Watson 60 (MO). HONDURAS. Comayagua: Standley 56117 (F, NY, US); Lempira: Allen 12264 (MO, TEFH); Morazan: Standley 325 (F); Olancho: Allen 12853 (MO, TEFH). COSTA RICA. Alajuela: Brenes 21861 (F); Cartago: Alfaro s.n. (F); Guanacaste: Alfaro 24 (F);

Heredia: Standley & Valerio 50485 (NY, US); San Jose: Stevens 13426 (MO).

PANAMA. Bocas del Toro: Allen 5337 (MO); Chiriqui: Allen 5375 (MO).

World range: Southeastern U.S.A.; Mexico; Central America; Western and Northern South America.

Campylopus zygodonticarpus is a fairly common but generally unrecognized species in Central America. It is a small plant with erect capsules and setaceous leaves that are erect at base and flexuous above when dry. The species has basal leaf cells that are enlarged and firm-walled juxtacostally but smaller and firm-walled at the margins, and ventral hyalocysts in the costa that are smaller than or only as large as the guide cells, poorly developed, frequently fugacious alar cells. These characters are extremely
variable and in a single collection, depending upon which leaves are examined, the basal cells may be firm or lax walled, the ventral hyalocysts smaller or little larger than the guide cells, and alar cells absent to moderately developed. The degree of fringing on the calyptrae is also variable: both fringed and unfringed calyptrae can occur in single collections.

Dicranum tuerckheimii has been treated as a synonym of Microcampylopus curvisetus, but the ciliate calyptrae and small ventral hyalocysts in the costa place it in the synonymy of C. zygodonticarpus.


Plants long and slender; stems interruptedly foliate, central strand absent, epidermal cells small, thick-walled; leaves slender, setaceous above; costa broad, in cross section with well-developed guide cells, dorsal and ventral stereid bands, ventral hyalocysts absent; leaf cells smooth, thick-walled; alar cells well-developed. Perichaetial leaves weakly sheathing. Dioicous. Setae long, straight or twisted; opercula long conic, as long as the capsule; annuli present; peristome well developed, ventral surface smooth. Calyptrae cucullate, entire at base. Spores papillose.

Even though no significant gametophytic differences separate Bryohumbertia from Campylopus, the genus can be recognized by its long, slender, interruptedly foliate stems. Frahm (1982a) defined the genus by its straight setae, long operculum, annulus, and the smooth ventral surface of its peristome teeth. Bryohumbertia is similar to Atractylocarpus (here treated as Dicranodontium) in its slender setaceous leaves, ventral and dorsal stereid costal cells, straight setae, long opercula, annulus, and peristome teeth. Bryohumbertia differs from Dicranodontium, in its inclusive sense, only in its shorter upper leaf cells and interruptedly foliate habit. It is at best a weakly segregated genus, not one of the first rank.

1. Juxtacostal basal leaf cells with straight cell walls; leaves serrulate above
   1. B. filifolia var. filifolia
1. Juxtacostal basal leaf cells porose; leaves sharply serrulate to dentate above
2. B. filifolia var. longifolia


Plants yellow-green; stems to 6 cm long, branching from the terminal comal tufts. Leaves when dry erect to appressed below, spreading above, concave at base, leaves of comal tufts linear-lanceolate, those between the comal tufts ovate-lanceolate, 10-16 mm long; margins serrulate above; costa long excurrent, dorsal surface strongly toothed above; upper laminal cells irregularly elongate, 20-30 um long, walls incrassate, not pitted; basal cells rectangular, narrower towards margin, 30-75 um long, walls thickened, not pitted; alar cells forming distinct groups of red-brown, thin-walled, bulging cells. Setae 15-17 mm long, yellow, smooth; capsules inclined, cylindrical, 1.5 mm long, ribbed when dry, yellow to red, neck weakly strumose; peristome teeth hyaline above, red below, teeth narrowly triangular below, abruptly filiform above, split 2/3 their lengths, dorsal lamellae vertically striate below, densely papillose above, ventral lamellae smooth, ventral trabeculae weakly papillose to smooth; opercula 1.5 mm long. Calyptrae 2.5 mm long. Spores 12-19 um.

Illustrations. Bartram (1949, Fig. 21 G-I); Florschutz (1964, Fig. 24 A-L, as C. nanofilifolius); Frahm (1978, Pl. 10); Frahm (1979, p. 174); Frahm (1991a, Figs. 7 A-B, 9 C, 15).

Habitat. Tree trunks, stumps and decaying logs; 600-1200 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: Cook & Doyle 29 (US); Baja Verapaz: Sharp 5187 (F); Huehuetenango: Steyermark 49734 (F). EL SALVADOR. Santa Ana: Carlson 962 (F). HONDURAS. Comayagua: Allen 11083 (MO, TEFH); Cortes: Allen 14219 (MO, TEFH). COSTA RICA. Cartago: Standley 33945 (US); San Jose: Skutch 2822 (US). PANAMA. Bocas del Toro: Allen 5056 (MO); Cocle: Croat 67277 (MO); Darien: Folsom 6395 (MO); Panama: Croat 13102A
World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

The species is recognizable in the field by its slender setaceous leaves and interrup-
tedly foliate, comal-tufted stems. The typical variety differs from var. longifolia by
its smaller size, serrulate leaves, and the presence of non-porose walled basal leaf cells.

2. Bryohumbertia filifolia var. longifolia

Plants larger and more robust than the typical variety. Leaves to 20 mm long;
margins serrate to dentate in upper 1/3; costa toothed on upper dorsal surface; basal
leaf cells elongate and porose. Sporophytes unknown.

Illustrations. None.

Habitat. Tree trunks and branches, vines, logs and soil along roadsides; 2000-2400
m.

Distribution in Central America. EL SALVADOR. Santa Ana: Watson 4 (MO).
HONDURAS. Comayagua: Allen 13931 (MO, TEFH); Cortes: Allen 14303 (MO, TEFH).
Morazan: Allen 12371 (MO, TEFH); Ocotepoque: Allen 14482 (MO, TEFH);
Olancho: Allen 12629 (MO, TEFH).
CARTA RICA. Alajuela: Crosby 10020 (MO);
Cartago: Crosby & Crosby 6087 (MO);
Heredia: Standley & Valerio 51638 (FH, NY, US);
San Jose: Crosby 9834 (MO).
PANAMA. Bocas del Toro: Allen 5114 (MO);
Chiriqui: Croat 33321 (MO).
World range: Central America.

This variety differs from the typical variety by its longer leaves, thicker-walled,
distinctly porose basal cells, and sharply serrate to dentate upper leaf margins. It has
the leaf form, leaf cellular pattern and marginal serrations of Campylopus atlanticus,
but that species is more robust and lacks a comal tufted habit. Large forms of var.
longifolia are similar to Campylopus weberbaueri and C. valerioi in having a comal-
tufted morphology. These species, however, are much more robust and have a more
extensive region of porose leaf cells. Furthermore, C. weberbaueri has quadrate upper
leaf cells, and C. valerioi has a distinctive basal hyaline leaf border.


Plants erect, large to medium; stems radiculose, densely tufted. Leaves crowded,
erect to secund, subtubulose, setaceous from a lanceolate base; margins serrulate in
upper third, entire below; costa to 2/3 the leaf width at base, long excurrent, in cross
section with dorsal and ventral stereo bands; median leaf cells linear, basal cells
rectangular; alar cells variously differentiated, frequently fugacious or fragile, not
auriculate. Dioicous or autoicous. Setae erect to slightly flexuous or strongly cygneo
when moist, erect and twisted when dry; capsules erect or inclined, weakly furrowed;
well developed annuli absent; stomata absent; peristome teeth divided, vertically
striolate below, papillose above; opercula long rostrate. Calyptrae cuculate, not
fringed.
Dicranodontium and Atractylocarpus are gametophytically identical, and they differ only in the degree of erectness of their moist setae. In Atractylocarpus the setae are erect to flexuous, in Dicranodontium they are cygneous. Williams (1913) synonymized the two on the basis of his observations on setal variability. Dicranodontium has narrowly setaceous leaves with short, ovate bases, broad, excurrent costa with dorsal and ventral stereid cells, linear leaf cells, differentiated alar cells, stems with a central strand and non-sheathing perichaetial leaves. It is separated from some members of Campylopus solely by its linear leaf cells. Pilopogon is also similar in its erect setae, broad costa, and habit. It differs from Dicranodontium in having shorter leaf cells, ciliate calyptrae, and sheathing perichaetial leaves.

1. Inner basal cells enlarged, thin-walled, non-porose, strongly contrasting with narrow, incrassate and porose outer basal cells; dioicous
   3. D. meridoniale
1. Inner basal cells not differentiated from the outer basal cells, either firm-walled or incrassate and porose throughout; autoicous
   2

2. Leaves broadly ovate at base; basal and median leaf cells incrassate and porose;
   alar cells well-developed; setae cygneous when wet
   1. D. intermedium
2. Leaves linear to shortly ovate at base; basal and median cells firm-walled, not or weakly porose; alar cells poorly developed, fugacious; setae erect to flexuous when wet
   2. D. longisetum


Plants medium sized, in loose, erect, greenish yellow tufts; stems moderately to
densely white or red-tomentose, to 5 cm long. Leaves evenly spaced, erect-spreading to falcate, concave below, tubulose above, narrowly lanceolate from a shortly ovate base, 8-11 mm long, apex sharply and densely denticulate; median leaf cells long rectangular, incrassate and non-porose or commonly porose; basal cells near the costa rectangular, incrassate and porose, the outer basal cells longer and narrower forming a short, hyaline border; alar cells well developed, red-brown, occasionally fugacious. Autoicous. Perigonia terminal on short branches (1.5-5.0 mm) below the perichaetia. Setae yellow becoming red, smooth, 10-13 mm long, twisted and erect when dry, cygnesque when wet; capsules smooth or weakly furrowed when dry, oblong, 2.0-2.5 mm long, lightly roughened at base; peristome yellowish becoming dark red, teeth 0.5 mm long, deeply divided (at times almost to the base), dorsal surface vertically striate; opercula 1.5 mm long. Calyptrae 3.0 mm long. Spores 20 um.

Habitat. Epiphytic on branches in subcanopy, on tree trunks, fallen logs and occasionally terrestrial; 2300-3505 m.

Distribution in Central America. GUATEMALA. Huehuetenango: Sharp 4954 (F,
The specific epithet refers to its intermediate position between Atractylocarpus and Dicranodontium: it has the autoicous sexual condition of the former and the cygneous setae of the latter. Dicranodontium intermedium has broad leaves, well-developed alar cells and incrassate, porose inner basal leaf cells. In D. longisetum the leaves are narrower, the setae straight or flexuous, and the alar cells fugacious. Dicranodontium meridionale has enlarged, thin-walled inner basal leaf cells that strongly contrast with the narrow, firm-walled marginal basal cells. Dicranodontium intermedium is likely to be mistaken for a Campylopus, but its linear upper leaf cells, autoicous sexual condition, and Dicranodontium-type costal cross-section remove the species from Campylopus.


Plants medium sized, greenish yellow, terricolous; stems 2-3 mm long. Leaves evenly spaced, erect-presssed to falcate-secund, concave, narrowly lanceolate from a short ovate base, setaceous above, 6-11 mm long; margins incurved, serrulate above, entire below, weakly bordered by narrow, elongate cells at base; basal cells rectangular, thin-walled, bulging near the costa, becoming narrow, elongate and firm-walled at the margins; alar cells in small, fugacious groups of reddish yellow cells.
Autoicous. Setae 10-20 mm long, erect to weakly flexuous, red; capsules erect, oblong, 1-2 mm long, lightly furrowed when dry, red; peristome teeth red, lanceolate, vertically striate below, papillose above; opercula 1.0-1.5 mm long. Calyptrae 2.0-2.5 mm long.

Illustrations. Bartram (1949, Fig. 23 A-C); Padberg and Frahm (1985, Figs. 35-41); Frahm (1991a, Figs. 1 D, 4 B, 7 D, 8 A, 9 D, 12, as Atractylocarpus longisetus).

Habitat. Terrestrial and on soil over rocks, rotting logs and occasionally tree trunks: 700-3500 m.

Distribution in Central America. GUATEMALA. Huehuetenango: Vogel B-9010 (MO). EL SALVADOR. Santa Ana: Watson 5 (MO). HONDURAS. Lempira: Allen 12268 (MO, TEFH); Olancho: Allen 12471 (MO, TEFH). COSTA RICA. Cartago: Crosby & Crosby 9332 (MO); Heredia: Crosby 9696 (MO); Limon: Davidse et al. 28763 (MO); Puntarenas: Davidse et al. 28535 (MO); San Jose: Crosby & Crosby 5736 (MO). PANAMA. Bocas del Toro: Gomez et al. 22426 (MO); Chiriqui: Crosby 4056 (MO).

World range: Mexico; Central America; Western and Northern South America, Brazil.

This is the only Central American species of Dicranodontium with erect setae. Dicranodontium meridionale also differs in its lax, thin-walled and bulging basal leaf cells that are sharply differentiated from the outer basal cells. Dicranodontium intermedium has broad leaves with strongly porose basal leaf cells and well developed alar cells. It can be confused with Campylopodiella stenocarpa (= Atractylocarpus costaricensis), which is a much smaller plant with softer, flexuous leaves, a well developed annulus, narrower and fully divided peristome teeth and a costa like that of Campylopodiella (q.v.).

Plants slender, forming deep silky turfs, yellow-green above, brownish below, moderately to densely red tomentose; stems 2-10 cm long. Leaves distantly spaced, erect-spreading to curved-secund, strongly concave, long and narrowly setaceous from a shortly ovate base, 8-10 mm long; margins incurved, densely spinose at apex, becoming denticulate in the upper one-third, entire below, bordered at base by several rows of narrow, elongate cells; upper cells long elongate-rhomboidal to linear, firm-walled, incrassate, pitted; basal cells near the costa forming a distinct group, short rectangular, enlarged, thin-walled, hyaline, outer basal cells narrow, elongate, firm-walled and pitted; alar cells well developed, reddish brown, at times fugacious. Dioicous (?). Sporophytes unknown.

Illustrations. Bartram (1928, Fig. 8 A-G); Frahm (1991a, Fig. 143).

Habitat. On tree trunks, rotting logs, moist rock cliffs, and terrestrial; 1100-2600 m.

Distribution in Central America. GUATEMALA. Chiquimula: Steyermark 31000 (F, FH); Huehuetenango: Sharp 4893 (MO, NY, US). HONDURAS. Cortes: Allen 14313 (MO, TEFH); Lempira: Allen 11449 (MO, TEFH); Morazan: Olson 84-51 (MO); Olancho: Allen 12701 (MO, TEFH). NICARAGUA. Granada: Croat 39150 (MO); Matagalpa: Castro 2520 (MO); Rivas: Granzow de la Cerda 1678 (MO). COSTA RICA. Alajuela: Liesner et al. 15630 (MO); Guanacaste: Hammel 17646 (MO); Heredia: Crosby 9865 (MO); Limon: Davidse et al. 28850A (MO); Puntarenas:

Hammel et al. 15080 (MO); San Jose: Valerio B50 (FH). PANAMA. Bocas del Toro: Allen 5700 (MO); Chiriqui: Crosby 4058 (MO).

World range: Central America; Western and Northern South America.

This is a slender species with narrow, setaceous, well-spaced leaves. Its most distinctive feature is found in the basal leaf cells where the enlarged, thin-walled and hyaline inner cells contrast sharply with the narrow, elongate, thick-walled outer cells. However, the degree to which the inner basal cells are differentiated is variable and
appears to be influenced by the age of the leaves: older leaves have thicker-walled cells. The median leaf cells of Dicranodontium meridionale are incrassate and porose, a character it shares with D. intermedium, but that species is more robust with broader leaves and porose inner basal cells. Dicranodontium longisetum has similarly shaped leaves, but it has weakly differentiated alar cells and is autoicous.

All reports of Dicranodontium denudatum (Brid.) Britt. and D. pulchro-alare Broth. from Central America can be referred here. In view of the variable nature of the inner basal cells within single collections of D. meridionale, this species may prove to be synonymous with D. pulchro-alare. Dicranodontium pulchro-alare is the older name.


Plants slender in loose to dense tufts; stems irregularly branched, equally foliate, sparsely radiculose at base, central strand well-developed. Leaves appressed when dry, erect-spreading when wet, lanceolate, subulate-acuminate above; costa broad, with dorsal and ventral stereids, smooth or ribbed at back; upper cells small, thick-walled; basal cells rectangular, thin-walled, frequently hyaline at extreme base and for some distance along the basal margin; alar cells not differentiated. Dioicous. Perichaetial leaves long sheathing. Setae elongate, erect; capsules cylindrical, straight; stomata absent; peristome teeth 16, filiform, densely papillose; annuli caducous; opercula long rostrate, erect. Calyptrae cucullate, ciliate at base.

Pilopogon is characterized by its long, sheathing perichaetial leaves, cylindrical, smooth, estomate capsules, and straight setae. It is gametophytically close to some Campylopus species. But Central American species of Pilopogon have undifferentiated alar cells, and no species of Campylopus has dorsal costal stereids as well as rectangular, thin-walled, hyaline basal cells that continue up the basal margin in V-shaped pattern. The appressed-leaf habit of Pilopogon also occurs in Aongstroemia, which has shorter setae, non-sheathing perichaetial leaves, and a narrower costa. Dicranodontium has longer upper leaf cells, leaves sharply contracted into long subulae, non-sheathing perichaetial leaves, and entire calyptra. Frahm (1983) has revised the genus.

1. Upper leaves with long hyaline awns
   2. *P. laevis*

1. Upper leaves without long hyaline awns
2. Upper and median leaf cells subquadrate to short rectangular; upper leaves with shortly excurrent costa; setae 5-10 mm long; capsules 1.0-1.5 mm long
3. P. tiquipayae

2. Upper and median leaf cells elongate-oval; upper leaves with excurrent costa as long as the lamina; setae 10-20 mm long; capsules 2-3 mm long
1. P. guadeloupensis


Plants variable in size, slender to medium or large, forming dense or loose turfs, yellowish green; stems erect, 1-15 cm long. Leaves evenly spaced, appressed wet or dry, subulate from a narrowly oblong base, 3-6 mm long; margins erect to incurved, entire except denticulate at apex; costa excurrent (upper leaves at times with costa excurrent, as long as the lower leaves), occupying 1/2 the leaf width at base, ribbed at back; upper leaf cells elongate-oval to oblong, incrassate, not pitted; median cells narrowly oblong; basal cells rectangular, hyaline, thin-walled, extending upward along the basal margins in a V-shaped pattern. Perichaetial leaves long sheathing, setaceous above, convolute at base, reaching from 1/2 to nearly the entire length of the seta.

Setae 10-20 mm long, smooth below, papillose at apex; capsules erect to inclined, cylindrical, 2-3 mm long, smooth; peristome teeth filiform, densely papillose, 300 um high; opercula 1.0-1.5 mm long.

Illustrations. Hooker (1818, Pl. 5); Bartram (1949, Fig. 23 G-J); Frahm (1983, Figs. 12-21); Frahm (1991a, Fig. 148).

Habitat. On rocks and soil along trails and road banks; 1300-3500 m.

Distribution in Central America. GUATEMALA. Huehuetenango: Sharp 4895 (F); San Marcos: Standley 86198 (F, FH). EL SALVADOR. Santa Ana: Watson 102 (MO).

HONDURAS. Comayagua: Allen 11028 (MO, TEFH); Morazan: Allen 12372 (MO, TEFH); Ocotepeque: Allen 14445 (MO, TEFH); Olancho: Allen 12703 (MO, TEFH).

COSTA RICA. Alajuela: Crosby & Crosby 6273 (MO); Cartago: Crosby & Crosby 6140 (MO); Heredia: Crosby 3873 (MO); Limon: Davidse et al. 28761 (MO); Puntarenas: Davidse et al. 28527 (MO); San Jose: Crosby & Crosby 6156 (MO).
PANAMA. Bocas del Toro: Allen 5239 (MO); Chiriqui: Allen 9115 (MO).

World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

This is the common species of Pilopogon in Central America. It is exceedingly variable, and when sporophytes are absent can be easily confused with P. tiquipayae. Pilopogon tiquipayae has erect-spread leaves, shortly excurrent costa that are distinctly mammillose on the upper dorsal surface, and subquadrate median and upper leaf cells. The two species can generally be distinguished, but because of the variability of P. guadeloupensis, careful examination is needed. The upper leaves in P. guadeloupensis sometimes have hyaline points that can cause confusion with P. laevis, but the upper leaves in that species are consistently long, hyaline hair-pointed. The peristome teeth of Pilopogon tiquipayae resemble those of Ditrichum, which is a much smaller plant having a narrower costa, non-sheathing perichaetial leaves, and non-fringed calyptrae.


Plants small, forming loose, reddish yellow to red brown tufts; stems erect, to 10 mm high. Leaves erect-appressed to erect-spread, narrowly lanceolate, 3-4 mm long, subulate; margins incurved above, entire; costa in upper leaves long-excurrent into hyaline, denticulate awns, dorsal surface above with lamellae 1 cell high; upper and median cells oval to rhomboidal, incrassate, non-porose; basal cells elongate rectangular, hyaline, thin-walled, extending up the basal margins in a V-shaped pattern. Dioicus. Sporophytes not seen, description from Frahm (1983). "Seta to 1 cm; capsule 2 mm long, dark brown, longly rostrate; peristome teeth 16, split to the base into filiform prongs. Spores yellowish, ca. 13 um in diameter, smooth. Calyptrae cucullate, ciliate at base."

Illustrations. Hegewald and Hegewald (1977, Figs. 5-8); Frahm (1983, Figs. 50-57); Frahm (1991a, Figs. 6 A, 150).

Habitat. On soil; 3460 m.

Distribution in Central America. COSTA RICA. Cartago: Kuhbier 334 (herbarium Frahm).

World range: Central America; Western and Northern South America.
Pilopogon laevis is distinguished by its long, hyaline, hair-pointed upper leaves. Although P. guadeloupensis sometimes has hyaline-tipped upper leaves, most of its leaf apices are concolorous. Pilopogon tiquipayae also has lamellae a single cell high on the abaxial costal surface, but its leaves are not hyaline-tipped. This species can be mistaken for Campylopus pilifer, which has hyaline-tipped leaves, costal lamellae, and ventral costal stereids. However, the lamellae in P. laevis are a single cell high, and its leaves have hyaline, thin-walled basal cells that continue up the margin in a V-shaped pattern.


   Plants small, yellowish green; stems erect, 1-3 cm long. Leaves erect-appressed to erect-spreading, narrowly lanceolate, 2.5-3.5 mm long, subulate; margins erect to incurved, entire below, sparsely serrate above; costa shortly excurrent, dorsal surface distinctly mammillose above; upper and median cells subquadrate to short rectangular, incrassate; basal cells shortly rectangular to subquadrate, hyaline, thin-walled, extending upwards a short distance along the margins in a V-shaped pattern. Setae 5-8(-10) mm long, yellow to red, rough at apex, smooth below; capsules erect to /---------------------------------\
3. Pilopogon tiquipayae                  Chorisodontium setaceum

inclined, cylindrical, 1.5-2.0 mm long; peristome teeth red, filiform, not divided or occasionally irregularly divided, densely papillose, 400 um high; opercula 1.0-1.5 mm long. Calyptrae 2.0 mm long. Spores spherical, 15-20 um, smooth to lightly papillose, yellow.

Illustrations. Herzog (1916, Pl. 15); Frahm (1983, Figs. 65-71); Frahm (1991a, Figs. 158-159).

Habitat. On soil; 2250-3800 m.

Distribution in Central America. GUATEMALA. Guatemala: Kellerman s.n. (US); Quezaltenango: Sharp 2210 (FH, MO, US); San Marcos: Steyermark 35657 (F, FH).
COSTA RICA. Cartago: Inoue, Bryophyta Selecta Exsiccata 839 (F, MO); Heredia: Alfaro 92 (FH, US); San Jose: Valerio 98 (FH). PANAMA. Chiriqui: Allen 9100 (MO).

World range: Central America; Western South America.

Previously reported only from South America, Pilopogon tiquipayae has been confused with P. guadeloupensis in Central America. It differs by its smaller plant, seta, and capsule size, its subquadrate to subrectangular upper and median leaf cells and its shortly excurrent costa. Pilopogon laevis has a similar areolation and costal structure but differs in having hyaline, hair-pointed leaves. Jerry Snider (University of Cincinnati) was the first to associate Ditrichum steyermarkii with Pilopogon, the type specimen of which agrees in all particulars with Pilopogon tiquipayae.

Dicranoideae


Plants medium to large in dense, erect tomentose tufts. Leaves linear-lanceolate; costa single, moderately broad at base, flaring at midleaf and occupying most of leaf. Setae erect; capsules erect, cylindrical.


Plants green to yellowish green tufts; stems erect, 4-10 cm long, branches few, irregular, simple, central strand small. Leaves evenly spaced, somewhat distant, erect-spreading when wet, erect-flexuous when dry, curved-secund, linear-lanceolate, oblong-ovate at base, setaceous above, 10-15 mm long, tubulose and remotely denticulate above; costa long-excurrent, moderately wide at base then flaring outward and occupying most of the leaf at middle, toothed at back near apex; upper leaf cells elongate to irregularly rhomboidal, incrassate, not pitted; lower cells linear, incrassate and pitted; alar cells strongly differentiated, extending to the costa, red-brown, rectangular to sub-quadrate, walls thin and more or less bulging. Dioicous. Sporophytes unknown.

Illustrations. Bartram (1928, Fig. 12 A-I); Frahm (1981, [Pl. 2]); Frahm (1989, Fig. 6 B).

Habitat. Terrestrial and epiphytic; 2300-3500 m.

Distribution in Central America. HONDURAS. Santa Barbara: Allen 11666 (MO, TEFH). COSTA RICA. Cartago: Holm & Iltis s.n. (MO); Heredia: Crosby 10924 (MO); Limon: Davidse et al. 29307 (MO); San Jose: Crosby 10954 (MO). PANAMA. Bocas del Toro: Davidse et al. 25397 (MO); Chiriqui: Allen 9091 (MO).

World range: Central America.

Variable in plant size, Chorisodontium setaceum can be quite robust; it has the
aspect of a Dicranum. Its lower leaf cells are linear, strongly incrassate and pitted, while its shortly elongate upper leaf cells are only incrassate. The species was originally described as a Dicranoloma, but there is no hint of a marginal leaf border. The feature of Chorisodontium that makes the genus immediately recognizable is found in its costa. In surface view the costa is moderately broad at the base — wider than is typical for Dicranum, narrower than is typical for Campylopus — but at midleaf it flares abruptly outward and nearly fills the upper leaf. Dicranodontium intermedium is similar in its robust size, setaceous leaf apices and porose basal cells, but its costa is uniformly broad throughout and its setae are cygneous.

Frahm (1989) placed this species into the synonymy of Chorisodontium wallisii (C. Mull.) Broth. var. speciosum (Hook. & Wils.) Frahm, but cited the Central American collections of the species under C. mittenii (C. Mull.) Broth. Furthermore, C. setaceum will not come out in his key. Until the problem is more carefully studied C. setaceum is here maintained as a distinct species. The type specimen photograph of C. setaceum in Frahm (1989) fails to convey, because of its small scale, the relative aspect of this plant.


Plants small to robust; stems tomentose, central strand present. Leaves lanceolate to ovate-acute, smooth or papillose at back, more or less subtubulose or grooved; margins serrate to entire; costa narrow, ending below the apex to percurrent to shortly excurrent, smooth or with serrate ribs at back; cells subquadrate to elongate, thick-walled, porose or non-porose; alar cells well developed. Dioicous. Setae erect, single or aggregate; capsules cylindrical, erect or curved and inclined; opercula rostrate; peristome teeth 16, divided to the middle. Calyptrae cucullate, smooth, entire.

The four Dicranum species in Central America represent two phytogeographic groups: Northern Hemispheric (D. flagellare and D. rhabdocarpum) and Southern Hemispheric (D. frigidum and D. peruvianum). Three of the species (D. flagellare, D. rhabdocarpum, and D. peruvianum) have the more or less erect capsules typical of the segregate genus Orthodicranum.
1. Upper leaf cells subquadrate, not porose; brood branchlets clustered in upper leaf axils
   1. D. flagellare

1. Upper leaf cells elongate, porose; brood branchlets absent
   2

2. Leaves over 10 mm long, narrowly long-acuminate; costa with two prominent, serrate ribs at back
   2. D. frigidum

2. Leaves less than 7 mm long, acute or broadly short-acuminate; costa smooth or weakly ridged at back
   3

3. Leaves entire, 2.5 mm broad, ovate-acute; costa spurred, smooth; plants over 10 cm high; setae aggregate
   3. D. peruvianum

3. Leaves serrulate above, 1.0 mm broad, ovate-acuminate; costa not spurred, weakly ridged at back; plants less than 5 cm high; setae single
   4. D. rhabdocarpum


   Plants small to medium sized, dull yellowish green; stems 1-3 cm long. Leaves crowded, falcate-secund or equally spreading when wet, crisped when dry, lance-acuminate or ovate-lanceolate, more or less roughened above at back, 2-3.5 mm long, acute; margins erect below, subtubulose above, serrulate near apex; costa percurrent to slightly excurrent; upper cells subquadrate, thick-walled, not porose; basal cells
rectangular, elongate, thick-walled; alar cells forming distinct groups, reddish brown, rectangular. Brood branches with minute appressed leaves commonly present in clusters in the upper leaf axils. Setae 10–20 mm long, yellow becoming brown with age; capsules exserted, erect, cylindrical, 2–3 mm long; opercula 1–2 mm long.

Illustrations. Grout (1937, Pl. 44 D); Bartram (1949, Fig. 28 G–I); Jennings (1951, Pl. 12); Hegewald (1977, Figs. 1–3); Smith (1978, Fig. 69 9–11); Crum and Anderson (1981, Fig. 92 D–F); Crum (1983, Fig. 29 D).

Habitat. On tree trunks, decaying logs and limestone; 1500–3450 m.

Distribution in Central America. GUATEMALA. Huehuetenango: Standley 81705 (F, FH); Quezaltenango: Sharp 2128 (FH); Totonicapan: Standley 65906 (F, FH, US).


World range: Subarctic America, Western and Eastern Canada, Northwestern, North-Central, Northeastern, and Southeastern U.S.A.; Mexico; Central America; Caribbean, Western South America; Northern, Southwestern, Middle, East, and Southeastern Europe; Caucasus, Soviet Middle Asia, Siberia, Soviet Far East, Mongolia, China, Eastern Asia; Indian Subcontinent.

Dicranum flagellare is recognized by its subquadrate, non-porose upper leaf cells and clusters of microphyllous branchlets. Dicranum rhabdocarpum is nearly the same size, but has stiffly erect to weakly secund leaves and elongate, porose upper leaf cells. Some species of Holomitrium have quadrate upper leaf cells, similarly shaped leaves, microphyllous brood branchlets and erect capsules; however, Holomitrium has /---------------------------\
1. Dicranum flagellare

Sheathing perichaetial leaves and entire peristome teeth. Plants of D. flagellare from Central America have relatively thick-walled basal cells (noted by Crum and Anderson (1981) in plants from Hispaniola) but otherwise fall within the variation exhibited by the species in North America.

Venezuela, Merida, Moritz s.n.

Plants robust, shiny yellowish green; stems reddish to white tomentose, 4-12(-22) cm long. Leaves crowded, flexuous-spreading or falcate-secund, commonly undulate, linear-lanceolate, 10-13 mm long, ovate at base, narrowly long-acuminate above; margins erect (occasionally incurved above), sharply serrate in upper half; costa percurrent or ending just below the apex, with two prominent rows of sharply serrate ribs on upper dorsal surface; upper cells linear-elongate; basal cells linear, all cells incrassate and pitted; alar cells forming distinct groups, rectangular, red-brown. Perigonia on dwarf males. Setae aggregate (1-4), to 6 cm long, red; capsules curved, nodding or horizontal, cylindrical, 3-5 mm long, red; opercula long rostrate, 3 mm long.

Illustrations. Bartram (1949, Fig. 29 E-H).
Habitat. On humus, rotting logs, and soil of roadsides, trailsides and cliffs, occasionally growing on tree trunks; 1000-3700 m.

World range: Mexico; Central America; Western and Northern South America, Brazil.

This robust moss is commonly over 10 cm high. It has long, lanceolate, lightly undulate leaves (over 100 mm long) with strongly serrate margins in the upper half, two prominent, sharply serrate ribs on the back of the costa, and long (to 6 cm) aggregate setae. Bartram (1949) considered it very close to Dicranum polysetum Sw. It is generally found at high elevations and is the most common Dicranum in Central America.
to reddish tomentose. Leaves evenly spaced, moderately distant, erect-spreading when dry, widely spreading when wet, at apex erect-apressed in more or less tumid buds, deeply concave, broadly ovate-acute, 5-7 mm | 2.5-3.0 mm, acute to cucullate; margins involute above, entire, marginal cells not differentiated; costa weak, ending below apex, frequently spurred, smooth; cells elongate-sigmoid throughout, incrassate and strongly porose; alar cells forming distinct groups, reddish brown, thick-walled. Pseudautoicous. Setae aggregate, 1-3 per perichaetium, to 3 cm long; capsules exserted, erect, cylindrical, 3 mm long, smooth; peristome teeth pitted; opercula 2.5-3.0 mm long. Spores ovoid, 17-20 um, rough.

Illustrations. Robinson (1967, Figs. 1-5).

Habitat. On moist soil; 3130-3200 m.


World range: Central America; Western South America.

This is the first report of this moss outside South America (Colombia, Ecuador and Peru). Its large size and broad, widely spreading, deeply concave leaves that are cucullate at the apex give the plants an aspect unlike any other Central American moss. Its nearest relation (Dicranum bartramianum Allen) is found in New Guinea (see Allen 1987). Other noteworthy features of D. peruvianum are its weak, commonly spurred costa, elongate, incrassate and porose leaf cells, multiple setae, and erect capsules.


Type. U.S.A., New Mexico, Santa Fe, Fendler s.n.

Plants small, pale yellowish green; stems erect, 1-2 cm (reported to 5 cm) long. Leaves crowded, evenly spaced, suberect to nearly straight when wet, erect-spreading to weakly flexuous when dry, ovate-lanceolate, 3-5 mm long, broadly and shortly acuminate; margins plane, serrulate above, marginal cells not differentiated; costa ending just below the apex, toothed dorsally above; cells incrassate and porose, upper
cells elongate to irregularly rhomboidal; basal cells rectangular; alar cells forming distinct groups, reddish brown, shortly rectangular, thin-walled. Setae single, 1.5-2.0 cm long, yellow or light reddish; capsules, erect, cylindrical, 3.0-3.5 mm long; peristome teeth reddish brown; opercula 1.5-2.0 mm long.

Illustrations. Sullivant (1849, Pl. 3 1-13); Grout (1937, Pl. 46 G 1-12); Bartram (1949, Fig. 29 A-D); Lawton (1971, Pl. 32 1-3).

Habitat. On soil; 2400-3768 m.

Distribution in Central America. GUATEMALA. Quezaltenango: Standley 67749a (F, FH).

World range: Northwestern and Southwestern U.S.A.; Mexico; Central America; Caribbean.

Dicranum rhabdocarpum is near D. flagellare in size, but that species has crispate leaves, and quadrate, non-porose upper leaf cells. Dicranum peruvianum and D. frigidum are much larger species. The shortly acuminate leaf apices of D. rhabdocarpum are also distinct. In D. frigidum the leaf apices are long and narrowly acuminate, while in D. peruvianum they are broadly acute and frequently cucullate.

Sullivant's (1849, reproduced in Grout 1937) illustrations of the leaf apex of D. rhabdocarpum are especially good.


Plants medium to large, in dense tufts; stems erect, densely foliate, central strand present. Leaves abruptly linear-lanceolate from an obovate, strongly clasping base, wide-spreading to squarrose, crispate when dry; costa shortly excurrent to percurrent; leaf cells smooth; basal leaf cells elongate-rectangular, thin-walled, hyaline, sharply contrasting with the small, thick-walled, quadrate upper leaf cells; alar cells not differentiated. Autoicous. Perichaetial leaves short. Setae elongate, single or aggregated; capsules erect; peristome teeth divided; opercula rostrate. Calyptrae cucullate, entire at base.
The genus is recognized by its moderately well-spaced leaves with high, shiny, tightly clasping leaf bases and strongly contrasting upper and lower leaf cells. It is similar to Holomitrium in its strongly clasping leaf bases, well differentiated upper and lower leaf cells, and erect capsules. Holomitrium differs in its pseudautocious condition, differentiated alar cells (at times fugacious), long sheathing perichaetial leaves and entire peristome teeth.

1. Leaves entire; capsules oblong; peristome teeth papillose on the outer surface; spores 40-50 um, papillose
   1. S. lindigii

1. Leaves serrate to crenulate above; capsules long cylindric; peristome teeth vertically ridged on outer surface; spores 12-20 um, smooth
   2. S. vaginata


   Plants yellowish green to brownish yellow, corticolous; stems 2-3 cm long, branches few, irregular, simple. Leaves evenly spaced, obovate below, linear-lanceolate above, 5-6 mm long, subulate; margins erect, entire; costa shortly excurrent to percurrent. Setae 7-10 mm long, yellow to reddish yellow; capsules oblong, 2.0-2.5 mm long, smooth, red; peristome teeth red, lanceolate, papillose on outer surface, 0.2-0.3 mm long; opercula 0.5-0.8 mm long. Calyptrae not seen. Spores ovoid, 40-50 um, papillose-warty, reddish.

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1. Symblepharis lindigii 2. Symblepharis vaginata

Illustrations. Salmon (1897-98, Pl. 26 33).
Habitat. On bamboo; 3130 m.
Distribution in Central America. COSTA RICA. San Jose: Crosby & Crosby 6122 (MO).
World range: Central America; Western South America.

This South American species (Colombia, Ecuador and Bolivia) differs from Symblepharis vaginata in its entire leaves, generally shorter setae, shorter, oblong capsules, large, warty spores, and broader, papillose peristome teeth. Although Salmon (1897-98) attributed most of these differing character states to forms of the variable S. vaginata, none has the entire suite of character states. The papillae on the outer surface of the peristome in S. lindigii are not arranged randomly but rather in vertical rows. This pattern is suggestive of the vertically striate peristome teeth of S. vaginata.


Plants green to yellow-green; stems 2-5 cm long, branches few, irregular, simple. Leaves evenly spaced, 6-7 mm long, squarrose-crisped when dry; margins denticulate to serrate above, erect; costa ending at the apex or shortly excurrent. Setae 1-3 per perichaetium, 5-25 mm long, yellow becoming red with age; capsules erect to slightly inclined, cylindrical, 3.0-4.5 mm long, smooth, yellow; peristome teeth red, linear-lanceolate, vertically striate, 0.5 mm high; opercula 1.0 mm long. Calyptrae 4 mm long. Spores ovoid, 15-20 um, smooth, yellow-green.

Illustrations. Salmon (1897-98, Pl. 25 1-23); Bartram (1949, Fig. 24 I-J).
Habitat. On tree trunks, branches and logs, occasionally terrestrial; 2400-4200 m.

World range: Southwestern U.S.A; Mexico; Central America; China; Indian Subcontinent.

Symblepharis vaginata is exceptionally irregular in many features. Its setae vary from 5 to 25 mm long, but surprisingly, the little variability in capsule length is not correlated with seta length. The leaves of S. vaginata are always serrate to some degree, and this feature alone separates it from S. lindigii. Salmon (1897-98) allowed a great range in spore size for S. vaginata, recognizing a variety with spores equal in size to those of S. lindigii. In Central America spore size in S. vaginata never approaches that of S. lindigii. The peristome teeth of S. vaginata are linear, deeply divided and vertically striate on the outer surface, while those of S. lindigii are broader, divided only 1/2 their length, and papillose.


Plants small to robust, tufted, yellow-green above, brownish below; stems erect, central strand present. Leaves typically erect at base, more or less clasping, keeled or concave above, erect spreading wet, crispate to spirally contorted dry; margins serrate to crenulate, rarely nearly entire; costa strong, percurrent or excurrent, smooth at back or with a few apical teeth; cells smooth, elongate and porose at base, distinctly shorter above; alar cells differentiated, persistent or fugacious. Pseudoautoicous. Perichaetial leaves sheathing to convolute at base, long setaceous above, at times reaching and overtopping the capsules; capsules erect, cylindrical to oblong; stomata present; opercula subulate-rostrate; peristome teeth undivided or fenestrated, densely papillose on the outer surface; annuli absent. Calyptrae long, cucullate, entire at base. Spores spherical, weakly papillose.
Holomitrium, Eucamptodontopsis, and Schliephackea form a generic complex of medium to large, commonly corticolous mosses marked by five morphological features: 1. a strong single costa, 2. well developed alar cells, 3. long, sheathing perichaetial leaves, 4. erect capsules, and 5. undivided peristome teeth. The genera are weakly segregated, and features that are characteristic of one member of the group commonly occur sporadically throughout the complex. Allen (1990a) treated the complex in detail. Hegewald (1978) provided a useful revision of Holomitrium in the Antilles.

1. Leaf margins subentire throughout or crenulate below, serrate at extreme apex
   2
2. Upper leaf cells quadrate with straight or wavy walls; basal leaf cells strongly differentiated from upper cells; setae 5-10 mm long
   3. H. pulchellum
3. Upper leaf cells elongate with sinuose walls; basal leaf cells grading into upper cells; setae 10-15 mm long
   4. H. sinuosum
4. 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 weakly to not porose
   1. H. arboreum
5. 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
6. Upper leaf cells elongate, the outer cell walls sinuose
   5. H. terebellatum
7. Upper leaf cells quadrate with straight cell walls
   5
5. Upper leaves over 10 mm long 2. H. longifolium
5. Upper leaves less than 7 mm long

6. Leaves abruptly narrowed from base, keeled above, concave below, bistratose at margins and medially in rows; occasionally with clusters of deciduous branchlets at apex 6. H. williamsii
6. Leaves gradually narrowed from base, keeled or canalicate and unistratose throughout; deciduous branchlets absent 3. H. pulchellum


Plants medium; stems 2-4 cm long. Leaves crowded, spreading when wet, strongly crisped when dry, keeled above, clasping at base, long linear-lanceolate from an erect, ovate base, 2-6 mm long, acuminate; margins plane, strongly dentate in the upper 2/3; costa percurrent to shortly excurrent, frequently toothed above on dorsal surface; cells occasionally bistratose above or on the upper margins, upper cells quadrate to subquadrate, walls thickened and straight, extending downward along the margins into the basal region; basal cells linear, strongly differentiated, incrassate, pitted, basal marginal cells short rectangular, not or weakly porose, wider than the inner basal cells; alar cells 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 4-5 mm long; peristome teeth linear-lanceolate, 0.4-0.5 mm high.

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

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

Distribution in Central America. BELIZE. Cayo: Bartlett 11691 (FH, MO, US);
Toledo: Gentle 6499 (MO). GUATEMALA. Alta Verapaz: Sharp 2956 (FH, MO, NY, US); Baja Verapaz: Turckheim 6909 (NY); Huehuetenango: Sharp 4905 (F); Jalapa: Steyermark 32552 (F, FH); Peten: Lundell 2679 (FH). HONDURAS. Atlantida: Standley 54188 (F, FH, US); Comayagua: Olsen 84-12 (MO); Lempira: Allen 11849 (MO, TEFH); Morazan: Standley 12364 (F); Olancho: Allen 12453 (MO, TEFH). COSTA RICA. Alajuela: Brenes 16219a (NY); Cartago: Standley & Torres 50893 (FH, US, NY); Guanacaste: Alfaro 120 (FH, US); Heredia: Crosby 3884 (MO); Limon: Davidse & Herrera 31048 (MO); Puntarenas: Davidse 24574 (MO); San Jose: Crosby & Crosby 6254 (MO). PANAMA. Bocas del Toro: Allen 5718 (MO); Chiriqui: Allen 5211B (MO); Cocle: McPherson 7658B-2 (MO); Colon: Crosby 10374 (MO); Darien: Hammel et al. 16522 (MO); Panama: Stinson 5392A (MO); Veraguas: Croat & Folsom 33934 (MO).

World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

Holomitrium arboreum is variable in most features. It is recognized by the rows of subquadrate leaf cells that extend along the margins from midleaf into the basal regions. Typically its leaves 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
1. Holomitrium arboreum

2. Holomitrium longifolium

cells are quadrate. Plants from Costa Rica and Panama (described as H. standleyi) have long, crispate leaves that are loosely erect at base, a shortly excurrent costa, weakly porose basal marginal cells, and elongate upper leaf cells.

Material from Belize and Guatemala have leaves with rows of bistratose cells either medially or on the upper margins. This feature is characteristic of H. williamsii and H. calycinum (Hedw.) Mitt., but in those species the median leaf cells do not run down the basal margins and the basal marginal cells are narrow, elongate, and strongly porose.


Plants medium to large; stems to 8 cm long. Leaves crowded, erect-spreading when wet, erect at base and crisped above when dry, gradually narrowed from an oblong, clasping base 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 1/2; costa excurrent, toothed at back above; upper leaf cells quadrate, homogeneous, walls evenly thickened, the outer walls straight; basal cells linear, yellow, 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.

Habitat. On trees and terrestrial; 1750-2000 m.

Distribution in Central America. COSTA RICA. Heredia: Croat 35554 (MO); San Jose: Crosby 9714 (MO).

World range: Central America; Western South America.

The long, setaceous leaves of this species are frequently broken at the apex. It is similar to Holomitrium 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 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.

Plants slender, forming compact cushions; stems 5-20 mm long. Leaves crowded, erect-spreading when wet, crisped and contorted with the apex more or less spirally twisted when dry, keeled to canaliculate above, linear-lanceolate, 3-7 mm long, acuminate, weakly clasping at base; margins erect, entire or weakly crenulate to toothed at the extreme apex, unistratose; costa smooth at back; upper leaf cells quadrate to rounded, inc rasterate with straight or wavy walls; basal cells linear, strongly differentiated, incrustate and pitted; alar cells weakly differentiated, fugacious and remaining on stem when leaves are removed, hyaline. Perichaetial leaves reaching mid-capsule. Setae 5-10 mm long, yellow; capsules oblong, 1.5 mm long; 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).

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


World range: Mexico; Central America; Western South America.

Holomitrium pulchellum is the smallest member of the genus in Central America. It and H. sinuosum are the only species with entire to irregularly crenulate leaf margins. The alar cells of H. pulchellum are poorly developed (at times absent or present only as a single row of differentiated cells) and commonly fugacious. This character state is also found in H. terebellatum and to a lesser degree in H. sinuosum. The latter two species are larger plants with sinuose, pitted upper leaf cells, weak differentiation between the upper and basal leaf cells, longer (over 10 mm) setae, and cylindrical capsules.
Most collections assigned here to H. pulchellum are larger than the type in all features, the leaf margins just above the basal cells have a few sharp serrations, the upper leaf margins are at times serrulate, the upper leaf cells have wavy walls and the basal cells are porose. This expression of H. pulchellum, also found in Venezuela and Peru, may represent an aberrant form of H. terebellatum or a distinct species.

Breedlovea chiapensis is gametophytically identical to the type expression of H. pulchellum. Sporophytically, the two differ in peristome teeth ornamentation. The teeth in B. chiapensis are randomly papillose above, but the papillae on the lower dorsal surface are arranged in vertical rows. In H. pulchellum the peristome teeth are randomly papillose throughout.


Plants medium to large; stems to 5-7 cm long. Leaves crowded, erect at base, spreading when wet, twisted and crispate above when dry, variably undulate on the margins, strongly concave to keeled, abruptly narrowed from an ovate base, broadly acuminate above, 8-10 mm long, acuminate; margins erect to incurved, crenulate below, serrate at extreme apex, unistratose throughout; costa percurrent to shortly excurrent, smooth or weakly toothed at back; upper leaf cells rectangular, incrassate, the outer and inner walls strongly sinuose, not pitted, grading imperceptibly into basal cells; basal cells linear-rectangular, incrassate, pitted and sinuose; 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. Perichaetial leaves reaching the capsule middle. Setae 10-15 mm long, yellow; capsules cylindrical, 2.5-3.0 mm long, brown; peristome reddish orange, teeth linear-lanceolate, densely papillose, 0.6-0.7 mm high; opercula 2.5 mm long. Calyptrae 4.5 mm long.


Habitat. Corticolous on trunks and branches, humicolous on roots of epiphytic plants, and terrestrial; 700-2920 m.
Distri

bution in Central America. COSTA RICA. Alajuela: Brenes 16218b (FH, NY); Puntarenas: Hammel et al. 15389 (MO); San Jose: Maxon & Harvey 7982 (FH, NY, US). PANAMA. Bocas del Toro: Allen 5597 (MO); Chiriqui: Allen 5434 (MO); Cocle: Folsom & Collins 6476 (MO); Panama: Crosby 4365 (MO).

World range: Central America; Western and Northern South America.

Holomitrium sinuosum is a robust species with broadly ovate, crispate leaves spreading from the insertion and strongly porose cells throughout the leaf. The rectangular upper leaf cells grade smoothly into the basal leaf cells. Except for a few serrations at the apex the leaf margins are crenulate.

Holomitrium terebellatum also has elongate, sinuose upper leaf cells and weak cellular differentiation between the basal and upper regions of the leaves. But, H. terebellatum has leaves oblong at base, irregularly rectangular to nearly quadrate leaf cells, and sharply serrate leaf margins. The South American H. flexuosum Mitt. differs in having quadrate upper leaf cells with straight cell walls. Schliephackea meteorioides and Eucamptodontopsis brittoniae are similar in size and in having upper cells not sharply differentiated from the basal cells. In S. meteorioides the leaves are sharply serrate throughout and in E. brittoniae the spirally contorted leaves have linear-rectangular upper cells.
5. Holomitrium terebellatum


Plants medium to large; stems erect, 3-6 cm long. Leaves crowded, evenly spaced, erect-spreading when wet, crisped and strongly contorted when dry, keeled above, concave below, generally spreading from the insertion, not or weakly clasping at base, oblong below, gradually narrowed and linear-lanceolate above, 7-9 mm long, narrowly acuminate; margins erect, serrate to denticulate from midleaf to the apex, unistratose; costa excurrent, toothed at back near apex; upper leaf cells rounded-rectangular to irregularly quadrate, incrassate with sinuose walls, not pitted; basal cells strongly differentiated, linear, yellowish, incrassate, pitted, those at the margins narrower than the interior cells; alar cells commonly fugacious, hyaline, thin-walled. Perichaetial leaves reaching to the capsule base. Setae 10-20 mm long, yellow; capsules erect, cylindrical, 2-3 mm long, brown; peristome 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).

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

Distribution in Central America. COSTA RICA. Alajuela: Brenes 11465 (NY); Cartago: Standley 39849 (FH, US); Heredia: Standley & Valerio 50101 (FH, US); Limon: Davidse et al. 28975 (MO); Puntarenas: Crosby 2645 (MO); San Jose: Crosby & Crosby 8596 (MO). PANAMA. Chiriqui: Maxon 5696 (US).

World range: Central America.

This is a robust species 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 alar cells of Holomitrium pulchellum and H.
sinuosum may be fugacious, but these species differ in having subentire to crenulate leaf margins. Holomitrium pulchellum is also 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 cell walls as well as cell lumina, and the alar cells are more commonly persistent. The South American Holomitrium flexuosum is very close, differing only in having straight-walled upper leaf cells and persistent alar cells.

1. Eucamptodontopsis brittoniae var. brittoniae
2. Eucamptodontopsis brittoniae var. mcphersonii

Plants medium; stems 2-3 cm long. Leaves crowded, erect-spreading when wet, strongly crisped when dry, keeled above, oblong-ovate and 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 2/3, irregularly bistratose at the margins and in patches throughout the lamina; costa dorsally toothed above; upper leaf cells rounded-quadrate, homogeneous, evenly thick-walled; basal leaf cells linear, yellowish, incrassate and pitted, those at the basal margins narrower than the interior cells; alar cells well-developed, persistent, reddish brown, hyaline near the costa. Deciduous, flagellate branches commonly in clusters in leaf axils at stem apex. Leaves closely imbricate-appressed, short, broadly obtuse with a blunt, rounded mucro; costa weak, ending well below the apex. Sporophytes not known.

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

Habitat. On tree trunks; 1850-2000 m.


World range: Central America.

Holomitrium williamsii is the only Central American species with apical clusters of flagellate branches. It can be confused with H. arboreum, but differs in having elongate, narrow, and porose cells along the upper basal leaf margin instead of quadrate cells. The Caribbean H. calycinum is closely allied. Both species have irregularly bistratose leaf margins and laminae, elongate and narrow basal marginal cells, an abrupt basal to median laminal cell transition and 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 are cuspidate and have strong, percurrent costa.

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

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. Schliephackea differs by its sharply serrate leaf margins, pendent habit and shorter upper leaf cells. In Eucamptodontopsis the leaves are moderately to widely spaced, the margins are crenulate above and the upper leaf cells are elongate.

1. Leaves linear-lanceolate, to 15 mm long
   1. E. brittoniae var. brittoniae

1. Leaves linear, 20-32 mm long
   2. E. brittoniae var. mcphersonii


Plants medium to large; stems 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 smooth to slightly roughened at back above, percurrent; upper leaf cells linear-rectangular, those at the margins distinctly shorter, more or less rhomboidal, incrassate and pitted, smooth; basal cells linear-rectangular, not sharply differentiated from the upper leaf cells, incrassate and pitted; alar cells strongly differentiated, incrassate, short-rectangular, reddish brown, weakly pitted. Sporophytes unknown.
Illustrations. Bartram (1928, Fig. 11 A-I).

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

Distribution in Central America. COSTA RICA. Alajuela: Brenes 16206.1 (NY);
Guanacaste: Hammel 17648B (MO); Heredia: Standley & Valerio 50505 (F, FH, NY, US);
Puntarenas: Gentry & Burger 2749D (MO); San Jose: Valerio 141 (FH, US).
PANAMA. Bocas del Toro: Allen 5624 (MO); Chiriqui: Allen 5381 (MO); Cocle:
McPherson 11245G (MO); Panama: Allen 4935 (MO); Veraguas: Hammel & Kress
8578 (MO, NY).

World range: Central America.

Variety brittoniae has shorter leaves that are markedly broader at base than those of var. mcphersonii. Holomitrium sinuosum is similar in its irregularly crenulate leaf margins and porose to sinuose leaf cells, but it differs in its crispate leaves, broadly ovate leaf bases, and rectangular upper leaf cells. Schliephackea meteorioides differs in its pendent habit, shorter upper leaf cells, and sharply serrate leaves.

2. Eucamptodontopsis brittoniae (Bartr.) Allen var. mcphersonii Allen, var. nov.

Type. Panama, Chiriqui, Fortuna Dam region, trail to Cerro Hornito (Pate de Macho), 8°45'N, 82°15'W, McPherson 13595B (MO, holotype; PMA, isotype).

A E. brittonia var. brittonia foliis longioribus differt.

Plants slender; stems to 6 cm high. Leaves evenly and widely spaced, spreading from just above the insertion, spirally contorted above, concave to tubulose, linear, to 20-32 mm long, apex long setaceous, base shortly clasping; margins remotely crenulate above, entire below; costa smooth to slightly roughened at back above, percurrent; all leaf cells linear, incrassate and porose; alar cells strongly differentiated, incrassate, short-rectangular, reddish brown, weakly pitted. Sporophytes unknown.

Illustrations. Figs. 1-6.
Habitat. On tree branches and humus of roadside bank; 1700-2200 m.
Distribution in Central America. PAMAMA. Bocas del Toro: Allen 5230 (MO);
Chiriqui: McPherson 13595B (MO, PMA).

World range: Central America.

The variety mcphersonii differs from the typical variety only in its exceptionally long, slender leaves. A noteworthy feature of both varieties is the nearly identical form of the upper and lower leaf cells. This variety is primarily epiphytic. Its occurrence on humus along roadside banks demonstrates an ability to maintain itself on the ground in areas of high moisture after the branch or trunk on which it normally grows has fallen.


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

Schliephackea is characterized by its pendent habit, long, porose basal leaf cells and sharply serrate leaf margins. Within the Holomitrium-complex only the pendent habit is unique to Schliephackea; however, its other two features are not found in combination in any other species of the complex.


Plants medium to large sized, greenish yellow; stems to 30 cm long. Leaves distant, more or less ranked, spreading at right angles to flexuous when wet, undulate below and spirally twisted above when dry, lanceolate from a broadly ovate base, 7-10 mm long, slenderly acuminate; margins erect to incurved, keeled above, serrulate in the upper 3/4; costa shortly excurrent, smooth throughout; upper leaf cells rounded-rectangular (at times elongate-rectangular or rarely subquadrate), irregularly quadrate at the margins, incrassate, pitted and sinuose; basal cells linear-rectangular, incrassate and pitted; alar cells strongly differentiated, red-brown, walls thickened. Perigonia on
dwarf males growing on tomentum of female plants. Perichaetial leaves reaching or surpassing the capsule. Setae 10-14 mm long, yellow; capsules cylindrical, 2.5 mm long, brown; peristome orange-red, lanceolate, ending in a long, fine, hyaline point, papillose, 0.5-0.6 mm high; opercula subulate rostrate, 2.0-2.5 mm long. Calyptrae 2.5 mm long.

Illustrations. None.
Habitat. Pendent from branches of trees and shrubs; 700-2600 m.

Schliephackea meteorioides             1. Leucoloma cruegerianum

Distribution in Central America. COSTA RICA. Alajuela: Brenes 16253 (F, FH, NY); Heredia: Crosby 10939 (MO); Puntarenas: Moran & Moran 5865 (MO); San Jose: Crosby 10952 (MO). PANAMA. Bocas del Toro: Allen 5746 (MO); Chiriqui:
The remarkable pendent habit of this species greatly aids in its recognition. However, Schliephackea meteorioides is distressingly variable in most features. Typically the leaves are widely spaced, flexuous above, and strongly spreading to almost circinate from a broadly ovate base. But, many collections have 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 strongly to not porose. The leaf margins can at times be weakly serrate and distinctly undulate when dry.

Eucamptodontopsis brittoniae and Holomitrium sinuosum differ in their irregularly crenulate lower leaf margins. Holomitrium terebellatum has fugacious alar cells. When found in the expression characterized by spirally contorted leaves, weakly serrate leaf margins, and leaf cells subquadrate and non-porose, S. meteorioides is nearly identical to H. flexuosum. The two species differ in the pendent habit and widely spaced leaves of S. meteorioides (plants erect and leaves closely spaced in H. flexuosum).


Plants slender to medium, pale green, in mats or tufts; stems erect, sparsely and irregularly branched, weakly tomentose; central strand absent. Leaves gradually subulate-lanceolate from an ovate base; margins subtubulose to incurved, serrate at apex, otherwise entire; costa narrow, excurrent, percurrent or ending just below the apex; upper cells pluripapillose, marginal cells smooth, narrow, hyaline forming a distinct border, widest near midleaf and frequently indistinct near the base; alar cells well developed, sometimes forming auricles. Dioicus. Setae erect; capsules cylindric, erect; opercula long and narrowly conic; peristome teeth 16, divided to middle or entire. Calyptrae cucullate.

Most species of Leucoloma have a distinctive pale greenish color, apparently the
result of their pluripapillose leaf cells. Papillae development is variable within the genus, and at least one West African species is epapillose. On the strength of its hyaline leaf limbidium Leucoloma has been aligned with Dicranoloma. However, its cellular areolation and erect capsules are more similar to those of the Holomitrium-complex. This relationship finds further support in the entire peristome teeth of L. tortellum.

1. Leaves crispate, bistratose above; apex thickened, broadly acute to obtuse, frequently broken; costa usually ending just below the apex
   4. L. tortellum
1. Leaves flexuous or curved secund, unistratose above; apex setaceous, not broken; costa percurrent or excurrent

2. Upper leaf cells elongate; basal cells strongly pitted
   2. L. mariei
2. Upper leaf cells quadrate to subquadrate; basal cells not porose

3. Leaves spreading to erect-spreading; margins incurved above; midleaf limbidium more than 10 cells wide and forming a strong contrast with the broad median band of chlorophyllose cells
   3. L. serrulatum
3. Leaves flexuous; margins tubulose above; midleaf limbidium less than 8 cells wide (frequently only 2-3 cells wide), not forming a strong contrast with the subquadrate median chlorophyllose cells
   1. L. cruegerianum


Plants small, whitish to glaucous green; stems fragile, 0.5-2.0 cm long. Leaves crowded, evenly spaced, flexuous to wide-spreading, lanceolate-subulate, 2.5-5 mm long, apex setaceous; margins tubulose above subtubulose to incurved below; entire throughout except for the sharply denticulate apex, limbidia at midleaf well developed, 6-10 cells, ending in the acumen, distinct at leaf base; costa percurrent, smooth to papillose above at back; upper leaf cells irregularly sub-quadrate, densely pluripapillose, walls thickened; basal cells elongate-rectangular, walls at times pitted, smooth to weakly papillose, grading into the upper leaf cells; alar cells enlarged and firm-walled, yellow-red. Setae 10-12 mm long, red; capsules erect, cylindrical, 2-3 mm long, smooth above, scabrose at base, red; stomata absent; peristome teeth red, lanceolate, striate below; opercula 1.5 mm long. Calyptrae 2.0 mm long, smooth. Spores rounded, smooth.

Illustrations. Bartram (1949, Fig. 30 E-H); Florschutz (1964, Fig. 27).

Habitat. On tree trunks and rotting logs, occasionally on damp bank and rocks; 80-2000 m.

Distribution in Central America. BELIZE. Cayo: Mains 4004 (F, US); Toledo: Davidse & Brant 32117 (MO). GUATEMALA. Alta Verapaz: Croat 41617 (MO); Peten: Lundell 2840 (NY, US); Quezaltenango: Standley 84880 (F, NY). HONDURAS. Comayagua: Allen 12337 (MO, TEFH); Cortes: Allen 14211 (MO); Morazan: Standley & Williams 771 (F); Ocotepeque: Allen 14541 (MO, TEFH); Olancho: Allen 12767 (MO, TEFH). NICARAGUA. Jinotega: Stevens & Miller 22503 (MO). COSTA RICA. Alajuela: Brenes 25 (NY); Cartago: Standley & Torres 51013 /-----------------------------------\
2. Leucoloma mariei

(NY, US); Heredia: Hatheway & Hatheway 1713 (US); Puntarenas: Gentry & Burger 2754F (MO); San Jose: Griffin & Morales B 112 (F, MO, NY). PANAMA. Bocas del Toro: Allen 5856A (MO); Chiriqui: Allen 5213 (MO); Coclé: McPherson 7972f (MO); Colon: McPherson 10263A (MO); Darien: Mori & Gentry 4479a (MO); Herrera: McPherson 10271B (MO); Los Santos: McPherson 13508G (MO); Panama: Tyson 2204, 2205 (NY); Veraguas: Mori & Kallunki 5368 (MO, PMA).

World range: Mexico; Central America; Caribbean, Northern South America.

Leucoloma cruegerianum is distinguished from L. serrulatum by its slender size, setaceous leaves and narrow leaf limbidium (never more than 8 cells and commonly only 2-3 cells wide at midleaf). The leaves of L. cruegerianum are variable in apex denticulation, limbidium width, and the development of cellular papillae. Material from Belize and Guatemala closely matches Caribbean material, but most other Central American collections represent the subimmarginatum-expression. In this expression the plants are smaller, the leaves more strongly flexuous and tubulose above, and the leaf border is weakly developed.


Plants medium sized, reddish green; stems 1-2 cm long. Leaves evenly spaced,
curved-secund, lanceolate-subulate, 3-5 mm long, subulate; margins incurved to subtubulose, entire, denticulate at the extreme apex, limbidia narrow and poorly defined above, 2-3 rows of cells at midleaf, merging with the basal cells below; costa percurrent to shortly excurrent, smooth to weakly papillose above at back; all leaf cells elongate and firm-walled, weakly pluripapillose above, smooth below; basal cells pitted; alar cells in bulging groups, reddish brown, firm-walled. Sporophytes unknown.

Illustrations. None.
Habitat. On tree; 100-250 m.
Distribution in Central America. BELIZE. Toledo: Davidse & Brant 31933 (MO).
HONDURAS. Comayagua: Allen 13877 (MO).
World range: Central America; Caribbean.

Leucoloma mariei resembles a large form of L. cruegerianum, but it differs in its elongate upper leaf cells and strongly pitted basal cells. Phylogenetically the species appears closest to L. serrulatum as judged by the similarity of its leaf cells to the basal and interior limbidial cells of L. serrulatum. Previously known only from Guadeloupe and Puerto Rico, the presence of L. mariei in Belize is a good example of the affinity of the moss flora in this region of Central America to that of the Caribbean.


Plants medium sized, pale greenish or reddish yellow; stems to 8 cm long. Leaves evenly spaced, wide-spreading to patent, often nearly straight or somewhat curved, secund at stem apex, linear-lanceolate, 4-7 mm long, narrowly subulate-acuminate to setaceous; margins incurved, sharply serrulate above, limbidia not reaching the apex, 2-3 cells wide in upper 1/3, increasing rapidly to 10-16 cells wide at midleaf and
contrasting sharply with the smaller interior cells; costa excurrent, papillose at back; upper leaf cells oblong, incrassate, short oblong along the costa in a broad band nearly to the leaf base; alar cells in bulging reddish groups of thin-walled, rectangular cells, commonly remaining on the stem when the leaves are removed. Asexual reproduction by means of deciduous leaves. Sporophyte not seen.

Illustrations. Bartram (1949, Fig. 30 A-D); Florschutz (1964, Fig. 25 A-G).

Habitat. On tree trunks and fallen logs, occasionally terrestrial; 20-2600 m.

Distribution in Central America. BELIZE. Cayo: Gentle 9186 (MO); Toledo: Davidse & Brant 32286 (MO). GUATEMALA. Alta Verapaz: Steyermark 45615 (F, NY); Baja Verapaz: Croat 41197 (MO); Chiquimula: Steyermark 31030 (F); Izabal: Steyermark 41765 (F); Quezaltenango: Steyermark 34350 (F); San Marcos: Sharp 5512 (F); Zacapa: Steyermark 29827 (F). HONDURAS. Atlantida: Standley 53184F (US); Comayagua: Allen 12306 (MO, TEFH); Cortes: Allen 14152 (MO, TEFH); El Paraíso: Valerio-Rodriguez 1939 (F); Lempira: Allen 11331 (MO, TEFH); Morazan: Standley & Williams 697 (F); Olancho: Allen 12563 (MO, TEFH); Santa Barbara: Crosby 2785 (MO). NICARAGUA. Granada: Almeda 1460c (CINC); Matagalpa: Davidse & Sousa 30508 (MO). COSTA RICA. Alajuela: Brenes 16178 (F, NY); Cartago: Valerio 224 (US); Guanacaste: Standley & Valerio 46457 (US); Heredia: Standley & Valerio 50135 (NY, US); Puntarenas: Crosby 9946 (MO); San Jose: Crosby 3732 (MO). PANAMA. Bocas del Toro: McPherson 6750B (MO); Chiriqui: Crosby 3993 (MO); Cocle: McPherson 12437 (MO); Colon: Crosby 10437 (MO); Darien: Mori & Gentry 4318 (MO); Herrera: McPherson 10305B (MO); Los Santos: Hammel 5396 (MO); Panama: Crosby 4457 (MO); Veraguas: Crosby 10283 (MO).

World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

Leucoloma serrulatum, a common and abundant species on tree trunks, has stiffly spreading leaves and a broad leaf limbidium that strongly contrasts with its short, papillose interior leaf cells. A careful examination of the leaf border indicates that the

true limbidium is restricted to the outermost 3-5 cell rows. The narrowly elongate, incrassate cells between the true limbidium and the short, interior cells represent an
extension of the elongated basal cells into the upper leaf (Florschutz's illustration of this feature is especially good). Leucoloma mariei has similar cells throughout the leaf, and their extensive development in L. serrulatum is indicative of a close relationship between the two species.

Frequently collections of this species are encountered with deciduous leaves that break off at the alar region; stems with such leaves are essentially naked below a short, apical cluster of leaves.

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4. Leucoloma tortellum                   Cynodontium guatemalensis


Plants medium sized, dull, yellowish green to brown-green; stems 1-2 cm long. Leaves crowded, evenly spaced, crisped to strongly flexuous when dry, ovate at base, gradually narrowed and linear above, 2.5-3.5 mm long, apex thickened and bistratose, blunt, broadly acute to weakly obtuse; margins incurved below, plane above, entire to obscurely crenate by papillae or sparsely denticulate at the extreme apex, limbidia at midleaf 1-3 rows of elongate hyaline cells, border not reaching the apex and merging with the basal cells below; costa ending below the apex or percurrent, papillose above at back; upper leaf cells quadrate to oblong, incrassate, densely pluripapillose; basal cells rectangular, incrassate, smooth; alar cells inflated, firm-walled, yellow-red. Asexual reproduction by thickened, fragile leaf tips. Dioicous. Setae red, 4-5 mm long;
capsules erect, oblong, roughened at base, red, 1-2 mm long; peristome teeth entire, reddish brown, weakly striate-papillose on dorsal surface at base, 125 μm long; opercula not seen. Calyptrae not seen. Spores lightly papillose, 17-22 μm.

Illustrations. Florschutz (1964, Fig. 25).
Habitat. On rocks in or near streams and on trees, 20-787 m.

Distribution in Central America. HONDURAS. Atlantida: Standley 53218 (F, US); Colon: Saunders 781 (MO). PANAMA. Chiriqui: Crosby 3971 (MO); Darien: Allen 8703 (MO); Herrera: McPherson 10306C (MO); Panama: McDaniel 6927 (NY, US). World range: Central America; Caribbean, Northern South America, Brazil.

Macroscopically Leucoloma tortellum resembles Holomitrium but has the papillose leaf cells and hyaline leaf limbidium of Leucoloma. Its strongly crispate leaves and thickened, bistratose, bluntly acute to obtuse leaf apices are distinctive, as is its occurrence on rocks in or near streams. The entire peristome teeth of L. tortellum are also encountered in Holomitrium.


Plants small, densely tufted, dull green or brownish. Leaves crispate when dry, lanceolate, keeled; margins recurved below, variously serrulate, bistratose above; costa ending below the apex, with 2 stereid bands; upper cells irregularly quadrate, often broader than long, unipapillose on both surfaces; basal cells rectangular, smooth; alar cells absent or slightly differentiated. Cladoautoicous. Perigonal buds just below the perichaetia. Setae elongate, cygneous; capsules erect, furrowed when dry; opercula rostrate; stomata present; peristome teeth 16, lanceolate, divided in the upper 1/2 to 2/3, red, vertically papillose-striate. Calyptrae cucullate.

Plants yellowish green above, brown below; stems to 3 cm long. Leaves erect at base, flexuous-spreading when wet, crispate when dry, keeled above, narrowly lanceolate, 5-6 mm long, acute; margins recurved below, irregularly doubly serrulate above; costa ending below the apex; upper leaf cells irregularly rounded-quadratde, thick-walled; basal cells rectangular, thick-walled, yellowish. Inner perigonal bracts acuminate. Setae 3-4 mm long, cygneous when wet, yellow; capsules erect, oblong-cylindrical, 1.0-1.5 mm long, erect, not strumose, furrowed when dry; peristome teeth red, divided 1/2 their lengths; opercula 0.5-1.0 mm long.

Illustrations. Bartram (1949, Fig. 24 D-H, as Oncophorus guatemalensis).
Habitat. On bark; 3000-3800 m.
Distribution in Central America. GUATEMALA. Quezaltenango: Steyermark 34872 (F, FH); San Marcos: Sharp 5391 (F, FH, MO).
World range: Central America.

Noteworthy features of this species include its bistratose, doubly serrulate leaf margins, coarsely unipapillose leaf cells, short, strongly cygneous setae, cladoautoioicus sexual condition, lack or near lack of alar cell differentiation, and strongly ribbed capsules. It appears close to Cynodontium alpestre (Wahlenb.) Mild., distributed in the U.S.A. and Europe, on the basis of its capsule characters, but that species has longer setae (6-7 mm) and rounded to rounded-obtuse perigonal bracts. The strongly cygneous setae in C. guatemalensis is of interest in documenting the multiple evolution of this character state in the Dicranaceae.

Rhabdoweisioideae


Plants small, in dense tufts or cushions, green above and brown below; stems without central strand. Leaves spreading when moist, strongly crisped when dry, narrowly linear lanceolate, keeled, acuminate; costa ending near apex, in cross section with well developed guide cells and dorsal stereid band, ventral stereid band absent or
weakly developed; upper leaf cells rounded quadrate, smooth; basal cells rectangular, hyaline; alar cells undifferentiated. Autoicous. Setae elongate, erect; capsules exserted, ovoid, 8-ribbed when dry; peristome single of 16 undivided teeth; opercula obliquely rostrate. Calyptrae cucullate.

Rhabdoweisia, revised by Lawton (1961), is similar to Amphidium in its leaf areolation, cell ornamentation, costal cross section, cucullate calyptrae, ovoid, strongly ribbed capsules, and the absence of a central strand in the stem. The two genera have been treated together in the Rhabdoweisiaceae (Anderson and Crum 1959). The peristome of Rhabdoweisia deviates in no significant way from that found in the Dicranales (Edwards 1979) and clearly Rhabdoweisia belongs in that order. Lewinsky (1976) placed Amphidium near the Orthotrichaceae because of the morphological similarity of its young sporophytes to those of Orthotrichum. However, because

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Lewinsky did not compare the morphology of young Rhabdoweisia sporophytes with those of Amphidium, the extent of the relationship between the two genera remains open

Plants small, loosely tufted; stems 2-3 mm high. Leaves to 2 mm long, linear-lanceolate, acuminate; margins plane or weakly recurved below, entire to minutely crenulate above; costa ending below the apex; upper leaf cells rounded quadrate; basal cells elongate, hyaline. Setae 2-3 mm long; capsules 0.5-0.8 mm long, ribbed when dry; opercula as long as the capsule; peristome teeth very fragile, smooth, filiform or subulate.

Illustrations. Hedwig (1801, Tab. 13 5-10); Husnot (1884, Pl. 5 1-7); Bartram (1949, Fig. 25 F-I); Lawton (1961, Figs. 1-10); Hegewald (1975, Fig. 3); Smith (1978, Fig. 53 1-4); Van Rooy (1991, Figs. 1-13).
Habitat. On soil; 2800-3400 m.
World range: Mexico; Central America; Western, Northern, and Southern South America, Brazil; Northern, Southwestern, Middle, East, and Southeastern Europe; Caucasus, Siberia; Macaronesia, Southern Africa.

The leaf cells of Rhabdoweisia fugax appear to have tiny markings that resemble the cuticular thickenings found in some species of Amphidium. Amphidium is eperistomate, while R. fugax has 16 short, filiform, fragile peristome teeth.
LEUCOBRYACEAE

Plants small to large, whitish to pale green, grayish or pale brown plants in dense cushions; stems with central strand absent or weakly developed. Leaves thick and fleshy, consisting mostly of an expanded costa; in cross section with 2–several layers of large empty, hyaline, porose cells (leucocysts) enclosing a central layer of small, green cells (chlorocysts); laminae narrow, consisting of delicate, hyaline, quadrate, oblong or linear cells. Asexual reproductive structures sometimes present. Dioicous, pseudautoicous or autoicous. Setae terminal, straight; capsules erect or inclined, at times strumose; peristome absent or single and consisting of 8 or 16 lanceolate teeth. Calyptrae cucullate or mitrate, entire or fringed at base with long, single-celled cilia.

The Leucobryaceae have thick, whitish leaves that consist mostly of an expanded costa. The costa is differentiated into outer layers of enlarged, hyaline leucocysts and a central layer of smaller green chlorocysts. A somewhat similar costal modification is found in the Dicranaceae (Campylopus, Brothera, Paraleucobryum). Furthermore, the peristome of Leucobryum is identical to that of Dicranum. For these reasons the two families are sometimes merged. Robinson (1985, 1990) attributed basic structural and functional features to the leucobryaceous leaf and on this basis redelimited the family. The important functional aspect of the leucobryaceous leaf involves its ability to generate and hold air within the leucocysts. This is thought to increase the photosynthetic efficiency of the completely enclosed chlorocysts.

1. Leaves flat or triangular in section above; chlorocysts in cross section in upper parts of the leaf triangular
   3. Octoblepharum
1. Leaves channeled above; chlorocysts in cross section in upper parts of the leaf quadrangular
   2

2. Leucocysts at base of leaf in a single layer above and below the chlorocysts; bud-like propagula commonly present; capsules immersed, hemispheric; peristome absent; calyptra mitrate
   2. Ochrobryum
2. Leucocysts at base of leaf in multiple layers (except L. martianum and L. subobtusifolium); reduced deciduous leaves sometimes present; capsules exserted, oblong-cylindrical; peristome present; calyptra cucullate

1. Leucobryum


Plants in compact or loose cushions or mats; stems simple or forked to irregularly branched, 1-20 cm high; central strand of small, thin-walled, frequently fugacious cells; rhizoids red-brown, on stems and from apex of leaves. Leaves appressed, imbricate, elliptic-ovate at base, erect-spreading, straight or flexuous, subtubulose, at times falcate-secund above, consisting mostly of a broad costa; apex acute or obtuse and cucullate; margins incurved above, entire, or weakly denticulate at the apex; cross section at base with a median row of small, green quadangular cells (chlorocysts) enclosed by 2-8 layers of enlarged, hyaline cells (leucocysts); leaf lamina present from leaf base to midleaf, consisting of a narrow (2-12 rows of cells) marginal band of hyaline, linear, long-rectangular, short-rectangular or quadrate, variably porose, firm-to lax-walled cells. Asexual reproduction by apical clusters of reduced, deciduous leaves. Pseudautoicous; male plants minute, growing on tufts of tomentum or leaves of female plants. Perichaetial leaves at times differentiated and shortly sheathing. Setae elongate; capsules cylindrical, curved or rarely erect, commonly strumose, ribbed or smooth when dry; stomata absent; annuli mostly nonrevoluble; peristome teeth divided 1/2 the distance to the base, vertically-striate, papillose or smooth on outer surface.

Calyptreae cucullate, entire.

Leucobryum is distinguished from Octoblepharum by its channeled leaves and quadrangular chlorocysts and from Leucophanes by its lack of costal stereids. Ochrobryum has a bizarre sporophyte and mitrate calyptrae, but has been chronically confused with Leucobryum in the absence of sporophytes. The combination of its small size, single layer of dorsal and ventral leucocysts, and upper chlorocysts subdivided to form chains of rounded to quadrate cells distinguish Ochrobryum from all species of Leucobryum except L. subobtusifolium. Vegetatively
the two differ only in the presence of bud-like propagula in Ochrobryum.

Leaf size, shape, and stature are important taxonomic characters in Leucobryum, as are characters found in the reduced leaf lamina and the number of leucocyst layers at the base of the leaves. In determining the leucocyst-layer number it is necessary to make leaf cross sections at the extreme leaf base. The glaucous green to whitish color of the plants makes the use of a contrast enhancing stain (e.g., crystal-violet) helpful.

There are eight species of Leucobryum in Central America. One (L. antillarum) is widely distributed. The others form two distributional groups, a predominately northern (Belize, Guatemala, Honduras, and Nicaragua) group and a southern (Panama and Costa Rica) group.

1. Leaf cross section at base with one ventral and one dorsal layer of leucocysts throughout

2. Plants medium sized, 10-30 mm high, reddish tinged; leaves falcate-secund, narrowly acute, 3-7 mm long; upper chlorocysts rectangular in surface view

   6. L. martianum

2. Plants small sized, 5-7 mm high, never reddish tinged; leaves straight, broadly acute to obtuse, 2-3 mm long; upper chlorocysts subdivided and forming chains of rounded to quadrate cells in surface view

   8. L. subobtusifolium

3. Patches of basal laminal cells irregularly subdivided into small, quadrate to rectangular cells forming a strong contrast with the larger, undivided more regular basal laminal cells; dorsal basal region of the costal surface with leucocysts numerous, small quadrate to rectangular

   4

3. Basal laminal cells not subdivided into smaller cells, consisting of uniformly linear
or large bulging rectangular cells; dorsal basal region of costal surface with leucocysts enlarged, bulging rectangular

6

4. Leaves greater than 5 mm long
2. L. antillarum

4. Leaves 2-4.5 mm long
5

5. Leaf lamina at midleaf with 3-4 rows of rectangular cells; leaf apex obtuse or cucullate, apiculate
5. L. incurvifolium

5. Leaf lamina at midleaf with 5-10 rows of short- to long-rectangular cells; leaf apex acute
7. L. polakowskyi

6. Leaves obtuse, apiculate, less than 4.5 mm long
5. L. incurvifolium

6. Leaves acute or acuminate, greater than 5 mm long
7

7. Leaves 5-8 mm long, crispate or spirally twisted when dry; leaf cross section with median region having only a single layer of ventral leucocysts
3. L. crispum

7. Leaves 8-25 mm long, spreading flexuous to secund when dry; leaf cross section with 2 or with patches of 2 layers of ventral leucocysts across the median region of the costa
8

8. Leaves 10-25 mm long; leaf bases 2.0-2.5 mm wide
4. L. giganteum

8. Leaves 8-13 mm long, leaf bases 1.0-1.5 mm wide
1. L. albicans
Type. Brazil, Beyrich.

Plants medium to large, whitish to glaucous green; stems to 4 cm high. Leaves erect at base, flexuous-spreading above, somewhat twisted when dry, 8-13 mm long, from an ovate base 1.0-1.5 mm wide, gradually or somewhat abruptly narrowed to long, narrow, strongly channeled upper limb; apex acute; margins erect to strongly incurved, entire or weakly denticulate above; costa in section near base with a median layer of chlorocysts and leucocysts in 1-2 ventral and dorsal layers toward the center and 2-3 ventral and dorsal layers at the margins, in surface view dorsal, basal leucocysts enlarged, rectangular and bulging; leaf lamina distinct from midleaf to the base, 6-9 rows of linear to long-rectangular, porose cells, basal cells not subdivided. Sporophytes not known from Central America.

Illustrations. Schwaegrichen (1826, Fig. 186).

Habitat. On tree trunks; 700-850 m.

Distribution in Central America. COSTA RICA. San Jose: Alfaro 153 (FH). PANAMA. Darien: Hammel 7280 (MO); Panama: Allen 9034 (MO).

World range: Mexico; Central America; Caribbean, Western, Northern, and Southern South America, Brazil.

Reliable identification of Leucobryum albicans requires sporophytes - it is reported to have a well-developed annulus - but plants with sporophytes have never been found in Central America. Its large size, undivided basal laminal cells and multi-layered basal dorsal and ventral leucocysts separate it from all species except L. crispum and L. giganteum. The former is a smaller species with crispate leaves and single layered ventral leucocysts in the basal, median leaf region. Leucobryum giganteum has generally longer leaves, but the two overlap in leaf size. The leaves of L. albicans are narrower at the base (1.0-1.5 mm) than those of L. giganteum (2.0-2.5 mm).

Plants medium, glaucous green, 3-5(-8) cm high. Leaves 5-8(-10) mm long, moderately spaced, flexuous-spreading to loosely falcate-secund, ovate-lanceolate, from an erect, ovate to oblong base, sharply tapering to a subtubulose upper limb, when dry the upper limb strongly concave, apex acute; margins erect to incurved below, strongly concave-incurved above, entire or denticulate at the apex; costa in cross section at the base with a median layer of chlorocysts, the leucocysts commonly in 3-4 dorsal layers and ventral 3-4 layers in the lateral regions and 1 ventral and dorsal layer in the median region, in surface view the dorsal leucocysts at the base of leaf commonly subdivided, forming irregularly quadrate to subrectangular cells identical in form to the subdivided basal laminal cells; leaf lamina well-developed, distinct to the base, 6-12 rows of long-rectangular to linear cells at the middle and 6-10 rows of short-rectangular cells at base, most of the basal leaf cells distinctly subdivided into irregularly quadrate to short-rectangular cells contrasting strongly with the undivided basal cells, cells porose above, porose or straight-walled below. Sporophytes not known from Central America.

Illustrations. Bartram (1949, Fig. 33 F-G).

Habitat. On tree trunks and branches, rotting logs, humus over rock and soil; 550-2680 m.

Distribution in Central America. BELIZE. Cayo: Mains 4010 (F); Toledo: Davidse & Brant 32261 (MO). GUATEMALA. Alta Verapaz: Standley 92321 (F); Baja Verapaz: Sharp 2865 (FH); El Progreso: Sharp 2737 (MO); Quezaltenango: Steyermark 33839 (F); Solola: Steyermark 47985 (F). HONDURAS. Comayagua: Allen 11065 (MO, TEFH); Cortes: Allen 14217 (MO, TEFH); Lempira: Allen 11346 (MO, TEFH); Morazan: Carlson 2635 (F, MO); Ocotepaque: Allen 14508 (MO, TEFH); Olancho: Allen 12684 (MO, TEFH); Santa Barbara: Allen 11642 (MO, TEFH).

NICARAGUA. Granada: Moreno & Lopez 7113B (MO); Jinotega: Grijalva & Araquistain 233 (MO); Matagalpa: Stevens 22190 (MO); Zelaya: Grijalva 370a (MO). COSTA RICA. Alajuela: Alfaro 77 (FH); Cartago: Crosby & Crosby 6362 (MO); Heredia: Crosby & Crosby 6535 (MO); Limon: Crosby 3692 (MO); Puntarenas: Busey 631 (MO); San Jose: Crosby & Crosby 6514 (MO). PANAMA. Bocas del Toro: Allen 5329 (MO); Chiriqui: Croat 16179 (MO); Cocle: McPherson 7694A (MO); Colon: Crosby 10455 (MO); Darien: Allen 8909 (MO); Panama: D'Arcy & Sytsma 14718 (MO); Veraguas: Crosby 10217 (MO, PMA).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean, Western and Northern South America.
Leucobryum antillarum, L. incurvifolium and L. polakowskyi form a complex marked by two basal leaf cell characters. First, most of the basal laminal cells are irregularly subdivided into triangular, quadrate or short-rectangular cells. The secondary nature of this cellular pattern is evident in that the pre-division cell boundaries can still be seen. Some basal cells remain long-rectangular and stand in marked contrast to the smaller subdivided cells. Second, the cells of the outer layer of dorsal leucocysts at the base of the costa are also subdivided into small, irregularly quadrate cells. In some collections nearly all the outer layer of dorsal leucocysts at base are subdivided, while in others only the leucocysts bordering the lamina are subdivided. Leucobryum polakowskyi and L. incurvifolium are smaller plants with leaves mostly only 2-3 mm long.

The base of the costa can have a large number of leucocyst layers in the lateral parts. This is a striking feature when well-developed, but the number of lateral leucocyst layers varies widely among populations. Leucobryum antillarum has the size and general aspect of the North Temperate L. glaucum (Hedw.) Angstr. in Fries. Leucobryum glaucum supposedly differs in having two layers of ventral leucocysts across the basal, median region of the leaf. The character is variable in both species.
2. Leucobryum antillarum


Plants medium sized, glaucous green to whitish, pale green (occasionally weakly reddish at base), 2-4(-5) cm high. Leaves 5-7(-9) mm long, closely spaced, flexuous-spreading to crispate when dry, weakly clasping from an ovate to obovate base, sharply contracted to a long, narrow, subtubulose upper limb, when dry strongly channeled above, apex acute; margins incurved, entire or lightly denticulate at the apex; costa in cross section at the base with a median row of chlorocysts and leucocysts in 2-3 dorsal and ventral layers in the lateral regions and 1 ventral and dorsal layer in the median region, in surface view the dorsal leucocysts at the base of leaf rectangular, enlarged, and bulging; leaf lamina well-developed, distinct to the base, of 7-10 rows of long-rectangular to linear cells, median cells porose, basal cells porose, basal cells not subdivided. Setae red, smooth, straight or flexuous, 10-15 mm long; capsules curved, 2 mm long, furrowed when dry, strumose; annuli non-revoluble; opercula rostrate, 2 mm long; peristome teeth red, 850-900 um long, cleft above, vertically striate and papillose on outer surface, weakly papillose on inner surface. Calyptrae 3 mm long. Spores 20-25 um, papillose.

Illustrations. Florschutz (1964, Fig. 34); Griffin (1979, Figs. 34-36).

Habitat. On rotting logs, soil or humus over rocks, and tree trunks; 580-1840 m.

Distribution in Central America. BELIZE. Cayo: Davide & Brant 33112 (MO).
HONDURAS. Comayagua: Allen 13917 (MO, TEFH); Cortes: Allen 14166 (MO, TEFH); El Paraiso: Rodriguez 1918 (F); Morazan: Standley & Williams 725 (F); Olancho: Allen 12856 (MO, TEFH). NICARAGUA. Granada: Croat 39151 (MO); Jinotega: Crosby 2735 (MO). COSTA RICA. Cartago: Standley 33880 (FH); San Jose: Crosby & Crosby 6373 (MO). PANAMA. Bocas del Toro: Allen 5181a (MO); Chiriqui: Salazar et al. 650 (MO); Cocle: Crosby 4379 (MO); Colon: Sytsma et al. 4289 (MO); Darien: Mori & Gentry 4350 (MO); Panama: McPherson 7105B (MO);
Veraguas: Crosby 10296 (MO, PMA).

World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

This species typically has crispate leaves that may be weakly reddish at the base and somewhat falcate-secund. These features are also seen in Leucobryum martianum, but that species has uni-layered leucocysts at the base of the leaf. A form of the species with long, weakly flexuous-spreading leaves closely matches those of the Brazilian L. sordidum Angstr. I can find no obvious differences between the species. In Central America this expression smoothly intergrades with typical L. crispum.

Leucobryum crispum is separated from L. albicans by its smaller size, more abruptly contracted leaf bases, and its leaves with a single layer of ventral and dorsal leucocysts in the median, basal region. From the L. antillarum-complex, L. crispum is best distinguished by its long rectangular basal laminal cells and enlarged, bulging leucocysts on the dorsal surface of its costa at base.


Plants large, glaucous green to yellow-green, 3-7(-13) cm high. Leaves (10-)13-20 mm long, erect-spreading to flexuous-spreading, occasionally secund, lanceolate, from an erect, weakly clasping, ovate base 2.0-2.5 mm wide, gradually or abruptly narrowed to a long subtubulose upper limb, when dry the upper limb weakly twisted and wavy at the margin, apex acute; margins incurved, entire or lightly denticulate at the apex; costa in cross section at the base with a median row of chlorocysts, the leucocysts commonly in 3 dorsal and 3 ventral layers in the lateral regions and 1-2
ventral and dorsal layers in the median region, in surface view the dorsal leucocysts at base of leaf rectangular, enlarged, bulging; leaf lamina well-developed, distinct to the base, of 4-10 rows of long-rectangular to linear cells, porose throughout, basal laminal cells not subdivided. Setae red, smooth below, papillose below the capsule, straight or flexuous, 18-22 mm long; capsules curved, 2 mm long, furrowed when dry, strumose; annuli non-revoluble; opercula rostrate, 2 mm long; peristome teeth red, 650-850 um long, cleft in the upper 2/3, vertically striate and papillose on outer and inner surfaces. Calyptrae 3 mm long, entire or lacerate at base. Spores 17-22 um, papillose.

Illustrations. Figs. 7-10.

Habitat. On humus (on ground, base of trees and roots of epiphytes), rotting logs, and tree trunks; 140-2200 m.

Distribution in Central America. HONDURAS. Olancho: Allen 12672 (MO, TEFH). COSTA RICA. Alajuela: Liesner et al. 15626 (MO); Cartago: Griffin et al. 182 (F, MO); Heredia: Crosby & Crosby 6548 (MO); Limon: Gutierrez 182 (F); Puntarenas: Crosby 2666 (MO); San Jose: Crosby 9733A (MO). PANAMA. Bocas del Toro: McPherson 8314C (MO); Chiriqui: Allen 5460 (MO); Cocle: Sytsma 1804 (MO); Darien: Folsom 6412 (MO); Panama: Crosby 10108 (MO); Veraguas: Crosby 10269 (MO).

World range: Mexico; Central America; Western and Northern South America, Brazil.

This is the largest Leucobryum in Central America, its long leaves (nearly all collections have some leaves over 13 mm long) separating it from other regional species. However, some Central American collections are intermediate in size between typical L. giganteum and L. albicans. These two species allegedly differ in plant size, the number of ventral leucocysts in the median region of the leaf at base, and the form of their annuli. Leucobryum giganteum is larger, has two full layers of ventral leucocysts in the median region of the leaf at base, and a poorly formed, persistent annulus. In contrast, L. albicans is smaller, has a single layer of ventral leucocysts in the median basal region of the leaf, and a well-developed annulus. In Central America not only are some collections intermediate in size, but the collections have basal,
median leaf regions that vary from being fully 2-layered to having only small, 2-layered patches. Central American collections with sporophytes have annuli of the giganteum-type.

4. Leucobryum giganteum

5. Leucobryum incurvifolium


Plants small, glaucous green to whitish, 1-2 cm high. Leaves 1.5-3.5 mm long, densely spaced, erect to erect-spreading, ovate-lanceolate, from a narrowly ovate base gradually or sharply contracted to a subtubulose upper limb, apex obtuse, cucullate, ending in a hyaline cell; margins strongly incurved, entire; costa in cross section at the base with a median layer of chlorocysts, leucocysts commonly arranged in 2 dorsal and 1(-2) ventral layers in the lateral regions and in 1 dorsal and 1 ventral layer in the median region, in surface view the dorsal leucocysts at base of leaf irregularly and
sporadically subdivided into quadrate to short-rectangular cells, upper chlorocysts subdivided and forming chains of rounded to quadrate cells; leaf lamina poorly developed, not distinct at midleaf, consisting of 4-6 rows of short-rectangular cells at base, basal cells sporadically and irregularly subdivided into quadrate to short-rectangular cells. Setae red, smooth, straight or flexuous, 8-11 mm long; capsules erect, 1 mm long, nonplicate, non-strumose; stomata absent; peristome teeth reddish brown below, hyaline above, 250 um long, cleft above, smooth to weakly papillose on outer surface, smooth on inner surface. Spores 17-23 um, smooth to obscuredly roughened.

Illustrations. Robinson (1965, Figs. 1-8).
Habitat. On roots of epiphytic plants, dead tree trunks, and soil over rock; 10-1500 m.
Distribution in Central America. BELIZE. Cayo: Mains 3893 (F); Corozal: Davidse & Brant 32555 (MO). GUATEMALA. Peten: Contreras 1328 (FH); Zacapa: Steyermak 42230 (F, FH). HONDURAS. Morazan: Standley 199 (F). NICARAGUA. Jinotega: Standley 9561 (F, FH).

World range: Southeastern U.S.A.; Mexico; Central America; East and South Tropical Africa.

Leucobryum incurvifolium is separated from all other regional species except L. polakowskyi by its small size. Leucobryum polakowskyi has a better developed lamina at midleaf (to 10 row of cells) and acute, non-apiculate leaf apices.
This species may be confused with sterile collections of Ochrobryum gardneri, which has the same size, type of leaf apex, and upper chlorocysts subdivided to form chains of rounded to quadrate cells. In Ochrobryum gardneri the dorsal and ventral
6. Leucobryum martianum              7. Leucobryum polakowskyi

leucocysts are in a single layer throughout the leaf, and that species commonly bears
globose, septate propagula at the tips of the leaves. Leucobryum incurvifolium
reproduces asexually by means of dense, apical clusters of reduced, decidous leaves.

The subdivision of the basal laminal cells in this species is not nearly as distinctive
as in L. antillarum or L. polakowskyi. This is the only Central American species of
Leucobryum with erect capsules.

6. Leucobryum martianum (Hornsch.) Hampe, Linnaea 17: 317. 1843. Dicranum
martianum Hornsch. in Mart., Fl. Brasil. 1: 11. 1840. Type. Brazil, Martius.

Plants glaucous green, 1-3 cm high. Leaves 3-7 mm long, commonly reddish
tinged particularly at the base, crowded and falcate-secund or occasionally erect-
spreading, long-lanceolate throughout or gradually narrowed from an ovate-lanceolate
base to a slender sub-tubulose acute apex; margins incurved, entire or sparsely
denticulate at the apex; costa in cross section at base consisting of a single layer of
dorsal leucocysts, a median chlorocysts, and a single layer of ventral leucocysts
throughout the leaf, in surface view the dorsal leucocysts enlarged, rectangular, not
subdivided; leaf lamina narrow, at times difficult to distinguish, consisting of 3-7 rows
of long-rectangular, firm-walled cells at mideleaf and 2-5 rows of short-rectangular cells
at base, basal laminal cells not subdivided. Setae red, smooth, straight or flexuous, 10-

15 mm long; capsules inclined to curved, 1 mm long, furrowed when dry, strumose;
annuli non-revoluble; opercula rostrate, 1.5 mm long; peristome teeth red, 525 um long, cleft above, vertically striate and papillose on outer surface, weakly papillose on inner surface. Calyptrae 2 mm long. Spores 15-22 um, smooth.

Illustrations. Bartram (1949, Fig. 34 A-C); Florschutz (1964, Fig. 33); Griffin (1979, Figs. 37-39); Griffin and Vareschi (1982, Figs. 14-20).

Habitat. On rotting logs, tree trunks, roots of epiphytic plants, and terrestrial; 18-1500 m.

Distribution in Central America. BELIZE. Cayo: Gentle 9185 (MO); Toledo: Gentle 5401 (MO). GUATEMALA. Izabal: Standley 72767 (F, FH). HONDURAS. Olancho: Allen 12852 (MO, TEFH); Yoro: Allen 13651 (MO, TEFH). COSTA RICA. Cocos Island [Puntarenas]: Itow (MO); Cartago: Standley & Valerio 46970a (FH); Limon: Sviha 3029 (FH). PANAMA. Bocas del Toro: Allen 5834 (MO); Canal Area: Willis 1 (F, MO, PMA); Chiriqui: Croat 33060B (MO); Cocle: McPherson 7694K (MO); Colon: Sytsma 2051 (MO); Darien: Mori & Gentry 4385 (MO); Panama: Allen 9026 (MO); Veraguas: Crosby 10231 (MO, PMA).

World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

In Leucobryum martianum the leaves are typically crowded, strongly falcate-secund, and reddish tinged at the base. In corticolous habitats the species has an erect spreading form. The reddish colored leaves are a good mark of the species. Leucobryum martianum differs from all other Central American members of the genus except L. subobtusifolium in having a single layer of dorsal and ventral leucocysts in the basal region of its leaves. Leucobryum subobtusifolium is a smaller plant with broadly acute to obtuse leaves.

Plants small, glaucous green, 1-2.5 cm high. Leaves 2.5-4.5 mm long, densely spaced, erect-spreading to flexuous-spreading, ovate-lanceolate, from a narrow or broadly ovate base abruptly narrowed to a subtubulose upper limb, apex acute; margins incurved, entire or lightly denticulate at the apex; costa in cross section at the base with a median layer of chlorocysts and the leucocysts in 3-4 dorsal and 3-4 ventral layers in the lateral regions, 1 dorsal and ventral layer in the median region, in surface view dorsal leucocysts at leaf base subdivided, quadrate to short-rectangular, upper chlorocysts subdivided and forming chains of rounded to quadrate cells; leaf lamina well-developed, distinct to the base, of 8-12 rows of long-rectangular to linear cells above, most basal laminal cells irregularly subdivided, triangular, quadrate or short-rectangular, sharply contrasting with larger, elongate-rectangular undivided basal cells, variously porose throughout. Sporophytes not known from Central America.

Illustrations. Bartram (1949, Fig. 33 A-C, as L. albidium, and D-E).

Habitat. On rotting logs, terrestrial, soil over rocks, and tree trunks (including pine bark); 150-2800 m.

Distribution in Central America. BELIZE. Cayo: Davidse & Brant 33086 (MO); Toledo: Davidse & Brant 32252 (MO). GUATEMALA. Alta Verapaz: Sharp 2957 (F, MO); Baja Verapaz: Croat 41343 (MO); San Marcos: Steyermark 36675 (F, FH); Solola: Steyermark 47985 (FH). HONDURAS. Atlantida: Standley 7977 (F); Comayagua: Allen 11022 (MO, TEFH); Lempira: Allen 11525 (MO, TEFH); Morazan: Olson 83-10 (MO); Ocotepeque: Allen 14454 (MO, TEFH); Olancho: Allen 12474 (MO, TEFH); Santa Barbara: Allen 11670 (MO, TEFH); Yoro: MacDougall et al. 3257A (MO). NICARAGUA. Esteli: Croat 42869 (MO); Jinotega: Standley 9921 (F, FH); Zelaya: Stevens 18722 (MO). COSTA RICA. Cartago: Alfaro 64a (FH); Heredia: Standley & Valerio 52169 (FH); San Jose: Standley & Valerio 48278 (FH). PANAMA. Chiriqui: D'Arcy 11112 (MO); Veraguas: Croat & Folsom 33938 (MO).

World range: Mexico; Central America; Caribbean, Western and Northern South America.

Leucobryum polakowskyi is separated from other Central American species of Leucobryum (except L. antillarum and L. incurvifolium) by the small, triangular,
quadrate or short-rectangular patches of basal laminal cells and by irregularly subdivided basal, dorsal leucocysts. Leucobryum antillarum and L. polakowskyi are nearly identical in most gametophytic features except leaf size (L. antillarum greater than 5.0 mm long, L. polakowskyi less than 4.5 mm long).

From Leucobryum incurvifolium this species is distinguished by its acute leaf apices and more extensively developed leaf lamina. In L. incurvifolium the leaves are obtuse, cucullate and apiculate and the leaf lamina at mideaf consists of only 3-4 rows of long, narrow, rectangular cells. The two species are sharply different in the erect capsules with smooth to weakly papillose peristome teeth of L. incurvifolium (curved capsules and strongly papillose teeth in L. polakowskyi), but the sporophytes of L. polakowskyi are unknown from Central America.


Plants small, glaucous green, 3-5 mm high. Leaves 2-3 mm long, erect at base, weakly flexuous above, lanceolate to narrowly ovate-lanceolate, gradually narrowed from base to apex; apex broadly acute to obtuse and apiculate; margins erect to incurved, entire; costa in cross section throughout the leaf with a single layer of dorsal leucocysts, a median layer of chlorocysts and a single layer of ventral leucocysts, in surface view the dorsal leucocysts enlarged, rectangular, not subdivided; upper chlorocysts subdivided and forming chains of rounded to quadrate cells; leaf lamina poorly developed, 1-2 rows of linear cells above, 2-4 rows of rectangular cells at base, basal cells not subdivided. Asexual reproduction by means of occasionally present apical clusters of small deciduous leaves. Sporophytes unknown.

Illustrations. None.
Habitat. On bark at base of tree; 800-900 m.
Distribution in Central America. PANAMA. Darien: Allen 8967 (MO, PMA).
World range: Central America; Brazil.
This species was recently transferred from Ochrobryum (Allen, 1992). Its sporophytes are unknown, and so its generic position is uncertain. Like Leucobryum it reproduces asexually by means of apical clusters of brood leaves. Ochrobryum reproduces asexually by means of globose propagula. It is similar to Leucobryum incurvifolium and like that species has short, rounded apical leaf chlorocysts. It differs from L. incurvifolium in having its dorsal and ventral leucocysts in a single layer throughout the leaf.

Excluded species

Leucobryum albidum (Brid.) Lindb.

All collections named this from Central America have been placed in either L. polakowskyi or L. incurvifolium. All three are small species with subdivided basal laminal cells and short, quadrate upper chlorocysts. From the former, L. albidum differs in the number of layers of ventral and dorsal leucocysts in the basal, lateral parts of the leaves: L. albidum 3-4 layers, L. polakowskyi 5-6 layers. Leucobryum incurvifolium has broadly acute to obtuse leaf apices, a weakly developed leaf lamina, and erect capsules with smooth to faintly papillose peristome teeth.


Plants small, 3-20 mm high, pale green to whitish; stems erect, simple or forked, central strand absent. Leaves erect-incurved, erect-spreading to flexuous, channeled; margins entire; costa in cross section at base with a median row of quadrate chlorocysts and single layers of dorsal and ventral leucocysts, at leaf apex chlorocysts hypocentric,
8. Leucobryum subobtusifolium 1. Ochrobryum gardneri

chlorocysts short in the upper region of the leaf, forming chains of rounded or quadrate cells; lamina narrow, restricted to the lower half of the leaf; alar cells not differentiated. Asexual reproduction by means of globose propagula clustered on short stalks on dorsal surface of leaf towards the apex or in leaf axils. Dioicous. Setae short; capsules immersed to shortly exserted, hemispheric to obconic, wide-mouthed when dry; annuli non-revoluble; stomata absent; opercula long-rostrate; peristome absent. Calyptrae long-rostrate, the rostrum more than twice the operculum length, mitrate, laciniate or ciliate-fringed at base.

This genus is recognized by its bizarre sporophyte and calyptra. In form the seta and capsule are nearly identical to the operculum, described (Robinson 1990) as "an inverted operculum . . . ." The calyptra is mitrate, generally ciliate-fringed, and has a rostrum as long as the operculum, capsule and seta combined. When detached, the calyptra (the operculum generally remains within the calyptra) looks very much like a sporophyte. The gametophytes of Ochrobryum resemble those of Leucobryum, but its leaves have a single dorsal and ventral leucocyst layer throughout, a feature also present in L. martianum and L. subobtusifolium. It is also distinctive in its asexual reproduction by means of globose propagula and in having apical leaf chlorocysts subdivided to form chains of rounded to quadrate cells (see Eddy 1990, Fig. 185 C). The genus has recently been revised (Allen 1992).
1. Leaves linear to setaceous, gradually narrowed from base to apex; apex mostly sharply acute, usually a few broadly acute; propagula clustered in leaf axils
   2. O. sessile

1. Leaves lanceolate, narrowly ovate at base; apex broadly acute or obtuse, both types in same collection; propagula on upper, dorsal leaf surfaces
   1. O. gardneri


Plants 3-13(-20) mm high. Leaves 2-5 mm long, 0.3-0.8 mm, closely and densely erect-patent or somewhat spreading, narrowly ovate-lanceolate to lanceolate, shortly acuminate, bluntly acute or rounded obtuse, at times cucullate, frequently apiculate; margins erect; costa with a single dorsal and a single ventral leucocyst layer throughout most of the leaf, apical ventral leucocysts multi-layered; leaf lamina narrow, of 2-4 rows of long-rectangular, variously porose cells at midleaf and 4-6 rows of rectangular, firm-walled cells at base. Asexual reproduction by brown, multicellular, globose propagula clustered on short stalks on the upper dorsal leaf surface. Setae smooth, 1.0-1.5 mm long; capsules immersed to emergent, 0.5-1.0 mm long; opercula 1.5 mm long. Calyptrae 4-5 mm long, ciliate or laciniate at base. Spores spherical, smooth or lightly roughened, 12-18 um.
Illustrations. Bescherelle (1897, Fig. 1, as O. gardnerianum, Fig. 5, as O. obtusifolium); Cardot (1900, Pl. 8 Fig. 37, as O. obtusifolium); Bartram (1949, Fig. 31 A-D, as O. obtusifolium); Robinson (1965, Figs. 15-21, as O. crumii); Yano (1975, Fig. 28 A-G); Allen (1992, Figs. 1-12).

Habitat. On rotting logs, tree trunks and bark at base of trees; 105-2200 m.


World range: Mexico; Central America; Western South America, Brazil; West Tropical Africa.

This species is marked by its bluntly acute to obtuse leaves that are distinctly swollen or thickened at the extreme apex. The leaf apices in Ochrobryum gardneri are remarkably variable, even within single collections. At times nearly all leaves are obtuse and apiculate; conversely, some collections have mostly broadly acute leaves. In all collections the leaves have thickened apices and at least some obtuse leaves. Globose propagula borne on the upper dorsal leaf surface are a constant, diagnostic feature of O. gardneri.

Ochrobryum sessile has moderately stout leaves with leaf apices that approach those of some plants of O. gardneri. It differs in its lack of an extensive region of multi-layered ventral leucocysts, propagula clustered in the leaf axils, and smoothly tapered, narrower, more sharply acute leaves.

Vegetatively, Ochrobryum gardneri resembles Leucobryum polakowskyi and L. incurvifolium. But, these species have multi-layered dorsal and ventral leucocysts at the base, quadrate basal laminal cells, and reproduce asexually by means of terminal clusters of reduced leaves.

Holomitriopsis laevifolia (Broth.) H. Robins., a Venezuelan species with obtuse, apiculate leaves and a single layer of dorsal and ventral leucocysts, may approximate this species. Holomitriopsis laevifolia is a more robust plant, lacks rounded to quadrate apical chlorocysts and leaf propagula, and has a cucullate calyptra and peristomate
capsule.
Mitten was the first to make the combination Ochrobryum gardneri. Although he used the name gardnerianum, it is an orthographic variant of gardneri and not an illegitimate name.


Plants 3-10 mm high. Leaves 4-5 mm | 0.2-0.5 mm, erect-patent to falcate, narrowly lanceolate, acuminate, ending in a single sharp, hyaline cell, flattened above and commonly spirally twisted when dry; margins erect to incurved below; costa with a single dorsal and a single ventral leucocyst-layer throughout most of the leaf, apical ventral leucocysts occasionally two-layered, for a single cell width; leaf laminae narrow, consisting of 2-3 rows of long-rectangular, variously porose cells at midleaf and 4-5 rows of elongate-rectangular cells at base. Asexual reproduction by hyaline or
brown, multicellular, globose propagula on short or long stalks usually clustered in the axils of the upper leaves, at times also in the lower leaf axils or on slender rhizoids at base of stem. Setae smooth, 1.0-1.5 mm long; capsules immersed to emergent, 0.7-1.0 mm long; opercula 1.5-2.0 mm long. Calyptrae 3-6 mm long, weakly ciliate at base. Spores spherical, lightly papillose, 15-18 um.


Habitat. On rotting logs or bark at base of trees; 700-2000 m.

Distribution in Central America. COSTA RICA. San Jose: Skutch 2209 (FH, MO, US); Puntarenas: Crosby 2658 (MO). PANAMA. Darien: Allen 8849 (MO, PMA); Panama: Castillo 112C (MO).

World range: Central America; Western and Northern South America.

Ochrobryum sessile is recognized by its narrow, frequently twisted leaves having setaceous to long acuminate apices. It has propagula clustered in the leaf axils and calyptrae that are weakly ciliate at base. It grades into the more narrow-leaved expressions of O. gardneri, but that species has larger, stouter leaves, some obtuse, swollen leaf apices, and leaf propagula on the upper dorsal surface of the leaves.

Leucobryum martianum is similar in having a single layer of ventral and dorsal leucocysts throughout the leaf, but it is larger plant with reddish, falcate-secund leaves and elongate-rectangular upper chlorocysts.

Octoblepharum
by Noris Salazar Allen

CARINAFOLIUM WILLIAMS IN GLEASON, BULL. TORREY BOT. CLUB 58: 502. 1931.

Plants glaucous green to yellow reddish to purple, dull to shiny, occasionally with a metallic luster; stems erect, sparingly branched. Leaves erect-patent, flexuous or reflexed above midleaf, ligulate, obtuse-apiculate to shortly acuminate, flattened or terete-triangular; margins entire to dentate, occasionally undulate at apex, limbidia present or absent; basal lamina with porate leucocysts in 1(-2) layers; median cross section of leaf with 3-4(-5) layers of leucocysts surrounding a central layer of mostly triangular to tear-drop-shaped chlorocysts. Autoicous or dioicous. Setae yellowish to dark orange-red, short or long; capsules oblong or cylindric, orange to dark red, phanerophore stomata at base; peristome teeth 8-16, smooth to vertically striate-reticulate or with semi-circular or bar-like thickenings, with or without trabeculae, outer and inner lamellae of 2(-3) rows of cells, prostome present; opercula rostrate, 0.5-1.8 mm long. Calyptrae cucullate, smooth, red at apex, stramineous below, 1.5-2.1 mm long. Spores yellow-green to brownish green, (15-)17.5-34.5(-50) um in diameter.

OCToblepharum is generally recognized by the presence in its leaf sections of a median layer of triangular chlorocysts. Each chlorocyst is surrounded by 3-4 leucocysts. Unlike Leucophanes the leaf does not have a midstereid band.

There has been sustained controversy over the systematic position of the genus. Traditionally the genus has been aligned with the Leucobryaceae on the basis of leaf structure. Fleischer (1904), stressing peristomal characters, placed it in the Leucophanaceae, near the Syrrhopodontaceae and Calymperaceae. Although the genus has been generally treated in the Calymperaceae for peristomal reasons (Andrews 1947, Robinson 1971, Crosby and Magill 1977, Magill 1981, Ellis 1985), Edwards (1979) concluded that the type of reduction seen in the Octoblepharum peristome "... leaves little clue as to relationships." Robinson's (1985, 1990) redelimitation of the Leucobryaceae, based on a consideration of leaf structure and function, included Octoblepharum in the Leucobryaceae.

There are seven species of Octoblepharum in Central America. Although some are variable and atypical collections may cause problems, all can be generally recognized by relative plant size (large, medium or small), habit (delicate, soft, sturdy), color (reddish purple or yellow-green), leaf fragility (commonly broken or intact), and peristome structure (ornamentation and number of teeth).

Central American distributions are based on the examination of specimens by Noris Salazar Allen and Bruce Allen.
1. Leaves fragile; midleaf cross section triangular-terete, equilaterally triangular with rounded edges; intact leaves to 20 mm or more long
   4. O. erectifolium

1. Leaves sturdy or fragile; midleaf cross section flattened, biconvex; intact leaves less than 11 mm long (to 15 mm in O. cocuiense)
   2

2. Leaves glossy, golden reddish brown or golden brown to orange-red at base, stramineous above; margins undulate-crenulate with prominent inflated leucocysts
   6. O. stramineum

2. Leaves dull, whitish green, pink or purple at base or purple throughout; margins rarely crenulate, with or without inflated leucocysts, rarely crenulate
   3

3. Plants soft; leaves keeled at base
   7. O. tatei

3. Plants rigid; leaves flat or concave at base
   4

4. Leaves sturdy, white-green to yellow-green or with a red to pink hue at base; peristome teeth 8
   5

4. Leaves fragile or if sturdy with some broken leaves, yellow-green, purple or light green above, purple below; peristome teeth 16
   6

5. Central laminal cells long hexagonal to rectangular; leaf apex dentate; capsules oval; setae 4-8 mm long; peristome teeth broadly triangular with faint, delicate trabeculae
   1. O. albidum

5. Central laminal cells quadrate; leaf apex more or less entire; capsules cylindric; setae greater than 10 mm long; peristome teeth lanceolate with thick, strongly projecting trabeculae
3. *O. cylindricum*

6. Leaves purple throughout or light green above, purple below with a dark pseudocostal area of elongate cells; upper laminal cells elongate hexagonal, strongly pitted

2. *O. cocuiense*

6. Leaves light green to yellow-green with a tinge of pink at base, without a pseudocostal area; upper laminal cells quadrate to short hexagonal in a distinct group, faintly pitted

5. *O. pulvinatum*


Plants in dense to loose turfs and cushions, glaucous green or with a pink to purple tone at base, 0.5-1.5(-3) cm high; stems sparingly branched, central strand absent. Leaves erect-patent to curved spreading, flattened, strap-shaped, apiculate, (3-)4-6(-8) mm long; margins with limbidia inconspicuous, 1-2 cells wide, sometimes undulate due to presence of marginal inflated leucocysts alone or in rows of 3-5 (or more); basal lamina with elongate hexagonal to rectangular leucocysts, in 1(-2) layers, pores narrow and inconspicuous; cross section of leaf at middle elliptic with a central layer of chlorocysts surrounded by 3-4 layers of leucocysts on each surface. Setae (2-)4-8 mm long, yellow to orange-red; capsules erect to subinclined, (0.5-)1-1.5(-2) mm long, oval, orange-red, darker and contracted at mouth; peristome teeth 8, triangular, smooth to vertically striate or reticulate, trabeculae and vertical lines faint and delicate or strong and prominent; opercula 0.5-1.2 mm long. Calyptrae to 1.5 mm long. Spores 20-25 um in diameter.

Illustrations. Dillenius (1741, Tab. 44 21); Hedwig (1801, Fig. 6); Cardot (1900, Pl. 13 61; Pl. 14 61); Fleischer (1904, Fig. 22 A-D); Bartram (1949, Fig. 32 A-D); Whittier (1976, Fig. 26 A-C); Breen (1963, Pl. 24 2-3, 5-8); Florschutz (1964, Fig. 39 A-H); Magill (1981, Fig. 44 1-9); Robinson (1985, Figs. 10-14); Costa (1988,
Fig. 5 A-F); Yano (1992, Fig. 18).

Habitat. On bark (particularly palms) at base of trees and shrubs, decomposing logs, soil and rocks; sea level to 2200 m, characteristically a lowland species, also occurring in upland forests.

Distribution in Central America. BELIZE. Belize: Davidse & Brant 33005B (MO); Cayo: Davidse & Brant 33038 (MO); Corozal: Davidse & Brant 32516A (MO); Orange Walk: Davidse & Brant 32734 (MO); Toledo: Davidse & Brant 32090 (MO). GUATEMALA. Baja Verapaz: Standley 69770 (F); Chiquimula: Steyermark 31226 (F); Izabal: Croat 41798 (MO); Jalapa: Standley 77411 (F); Peten: Morgan 26 (MO); Retalhuleu: Standley 88546 (F); Santa Rosa: Standley 78030 (F). EL SALVADOR. Ahuachapan: Winkler 26 (MO); Santa Ana: Winkler 33 (MO). HONDURAS. Atlantida: Yuncker 7990 (MO, NY); Comayagua: Allen 10979 (MO, TEFH); Cortez: Standley et al. 7072 (F); Intibucu: Allen 11093B (MO); Lempira: Allen 11830 (MO, TEFH); Morazan: Standley 226 (F); Olancho: Allen 12917 (MO, TEFH); Yoro: Allen 13585 (MO, TEFH). NICARAGUA. Jinotega: Standley 10216 (F); Managua: Standley 8778 (F); Masaya: Stevens 5288 (MO); Zelaya: Stevens 7791 (MO). COSTA RICA. Alajuela: Crosby 3825 (MO); Cartago: Alfaro (F); Guanacaste: Alfaro 25b (F); Heredia: Grayum 9633 (MO); Limon: Alfaro 74a (F); Puntarenas: Gomez 20035 (MO); San Jose: Nee 14029 (MO). PANAMA. Bocas del Toro: Antonio 3170 (MO, PMA); Chiriqui: van der Werff & Herrera 631A (MO); Colon: Dressler & Lewis 3740A (MO); Canal Area: Croat 7801 (MO, PMA); Darien: Allen 8936 (MO); Panama: Hammel 5553 (MO, PMA); San Blas Comarca: McPherson 11061A (MO); Veraguas: Antonio 2321 (MO).

World range: Southeastern and South-Central U.S.A.; Mexico; Central America; Caribbean, Western, Northern, and Southern South America, Brazil; China, Indian Subcontinent, Indo-China, Malesia; West, West-Central, East, and South Tropical Africa, Southern Africa, Western Indian Ocean; Australia; Northwestern, North-Central, Southwestern, and South-Central Pacific.

Octoblepharum albidum is the common Octoblepharum species in Central America. It is generally easy to recognize, but it is a variable species with some forms that have cylindrical rather than oval capsules, smooth triangular teeth, and short hyaline laminal
cells. There is also a form with leaves that are dark purple at the base and a peristome with vertical striations (e.g., Salazar 6588, PMA). The species is marked by its sturdy leaves, yellowish green color and short setae. It may be confused with O. cylindricum, which differs in having setae over 10 mm long, cylindrical capsules, strongly trabeculate peristome teeth, and entire leaf apices.

Octoblepharum perforatum C. Mull., Hedwigia 34: 119. 1895. Type. Brazil, Ule 1546 (H).
Octoblepharum pulvinatum (Dozy & Molk.) Mitt. var. angustifolium Broth., Hedwigia 45: 263. 1906. Type. Brazil, Ule 2339 (H).

Plants erect in compact turfs or cushions, purple-red to light green with a pinkish hue, 2-6.5 cm high; stems sparingly to highly branched, densely foliose, moderately red-tomentose. Leaves fragile, erect-patent to slightly spreading, ligulate, flattened with a dark, central pseudocostal area of elongate chlorocysts, obtuse and apiculate to acuminate, (4-)7-12(-15) mm long; margins smooth to undulate or dentate at apex, 1-2 cells wide; basal lamina abruptly widened, cells conspicuously pitted, elongate hexagonal at border, quadrate and slightly inflated towards center and elongate rectangular near the costa, large perforations on the abaxial and adaxial basal walls; leaf cross section at middle elliptic, with 3(-4) layers of leucocysts on each side of the central chlorocysts, at apex with one layer of leucocysts on each side of the chlorocyst layer. Setae 11 mm long, dark red; capsules cylindric, 1.7-2.6 mm, dark red, darker at mouth; peristome of 16 linear, orange-red to yellow-orange teeth, deflexed when wet,
2. Octoblepharum cocuiense

erect when dry, with semi-circular to circular thickenings on the outer lamellae; opercula 1.8 mm long. Calyptrae 2 mm long. Spores brown-green, 30-45(-50) um in diameter.

Illustrations. Cardot (1900, Pl. 14, as O. fragillimum); Bartram (1949, Fig. 32 J-K, as O. mittenii); Florschutz (1964, Fig. 37 A-B); Griffin (1979, Figs. 40-43); Yano (1992, Fig. 21).

Habitat. Epiphyte on bark of trees, particularly palms, also on rocks and soil; 400-1000 m.

Distribution in Central America. BELIZE. Cayo: Bartlett (FH). HONDURAS. Yoro: Allen 13464 (MO, TEFH). COSTA RICA. Cartago: Crosby 3819 (MO); Limon: Crosby 3667 (MO). PANAMA. Chiriqui: Salazar 8951 (PMA); Cocle: Antonio 3708 (MO); Colon: Kennedy 2799A (MO, PMA); Panama: Allen 4936 (MO, PMA); Veraguas: Crosby 10218 (MO, PMA).

World range: Central America; Western and Northern South America, Brazil.

Octoblepharum cocuiense is a large species marked by its distinctive reddish purple color, fragile, erect-patent to spreading leaves, and strongly pitted, porose basal laminal cells. It is the only Central American species with leaves having a central pseudocostal region of darkened, elongate cells.

Plants in dense tufts, glaucous green, pinkish towards base, 0.5-1.5(-2) cm high; stems sparingly branched. Leaves erect to curved outwards above middle, flattened dorsiventrally, strap-shaped, apiculate to shortly acuminate, not fragile, 4-6(-8) mm long; margins conspicuous at apex, 1-2 cells wide, entire to undulate towards apex, rarely toothed; basal hyaline lamina gradually tapering to the costal area (at least one side) with quadrate leucocysts at center and next to costa, short hexagonal cells near border, quadrate to rectangular at base; cross section of leaf elliptic, with a central layer of chlorocysts surrounded by 2-3 layers of leucocysts. Setae smooth, (8-)10-18(-20) mm long, straw-colored to light orange-red; capsules long cylindric, erect to arcuate or subinclined, urn slightly contracted below mouth, 1.5-2 mm long; peristome teeth 8, with thickened midline and trabeculate, and diagonal to vertical striations; opercula long rostrate, obliquely curved, to 1.1 mm long. Calyptrae to 2 mm long. Spores 8-21 um in diameter, strongly granular.

4. Octoblepharum erectifolium
5. Octoblepharum pulvinatum
Octoblepharum cylindricum differs from O. albidum by its longer setae, cylindrical capsules, entire leaf apices, and strongly trabeculate peristome teeth. It is distinguished from all other Central American species by the combination of a whitish green color, sturdy leaves, and eight peristome teeth.

4. Octoblepharum erectifolium Mitt. ex Williams, N. Amer. Fl. 15: 162. 1913. Type. Trinidad, Cruger (NY).

Plants in dense to loose turfs, whitish green to yellow-green, to 4.5 cm high; stems unbranched or sparingly branched. Leaves fragile and commonly broken in upper half to two thirds, intact leaves erect to curved, more than 20 mm long, in cross section terete-triangular at the middle, apiculate to shortly acuminate; margins with limbidia conspicuous at apex, 2-4 cells wide, more or less crenate to dentate; basal lamina gradually tapering to the costal area, leucocysts elongate, rhomboid, shorter on apical margins, finely pitted; cross section of the leaf at apex with 2 layers of leucocysts on each side of the chlorocyst layer, at middle with a central layer of chlorocysts surrounded by 4-6 layers of leucocysts on each side. Setae to 16 mm, orange; capsules to 2 mm long, erect to subinclined, orange to orange-brown, darker at rim; peristome of 8 elongate, reddish teeth with pronounced trabeculae and reticulate ornamentation; opercula to 1.2 mm long. Calyptrae and spores not seen.
Distribution in Central America. BELIZE. Cayo: Allen 15057 (MO).
GUATEMALA. Alta Verapaz: Standley 91692 (F, FH); Baja Verapaz: Sharp 5199 (F, FH). HONDURAS. Cortes: Allen 14332 (MO, TEFH); Olancho: Allen 12756 (MO, TEFH). NICARAGUA. Granada: Henrich & Moreno 194 (MO). COSTA RICA. Cartago: Crosby & Crosby 6318 (FH, H, MO); Heredia: Standley & Valerio 49653 (FH, H); Puntarenas: Nee & Mori 3573 (MO); San Jose: Crosby & Crosby 6396 (MO).
PANAMA. Bocas del Toro: Allen 5699 (MO); Canal Area: Crosby 3945 (MO, PMA); Chiriqui: Salazar et al. 9071 (PMA); Darien: Salazar & Gradstein 9356 (PMA); Panama: Gentry & Dwyer 5595 (MO, PMA).
World range: Central America; Caribbean, Western and Northern South America, Brazil.

The intact leaves of *O. erectifolium* are the longest of any *Octoblepharum* species in Central America. However, the leaves are exceedingly fragile and nearly always broken. The species is marked by its greenish yellow color and stiffly erect leaves that are terete to triangular in cross section. It is likely to be confused only with large forms of *O. pulvinatum*, which differs most clearly in having an elliptic leaf cross section and distinct quadrate to short hexagonal upper laminal cells.


Plants in loose to dense turfs, glaucous green, occasionally with a tinge of pink, 0.8-2 cm high; stems with erect, more or less parallel innovations. Leaves fragile or if sturdy some broken, erect-spreading to flexuous-secund, shiny with a broad hyaline lamina abruptly narrowed to the strap-shaped upper leaf, mucronate to nearly truncate, 5-8(-9) mm long; margins entire, sharply to inconspicuously and obtusely dentate at apex, smooth below, slightly undulate above; upper laminar cells irregularly short hexagonal, quadrate or pentagonal, 45-50(-60) um in longest dimension, pits narrow and inconspicuous; leaf cross section elliptic at middle, central layer of chlorocysts
surrounded by (2-)3 layers of porose hyaline cells on each surface. Setae 5.4-7.5 mm long, light yellow above, orange-red below; capsules erect to subinclined, 2-2.5 mm long, cylindrical, orange-red, slightly contracted under mouth, bulging papillose at base; peristome of 16 elongate, paired teeth, articulate, light orange to yellowish to pellucid, trabeculate with papillose, bar-like thickenings and central circular depressions; opercula to 1 mm long. Calyptrae to 2.1 mm long. Spores 15-18 um in diameter.

Illustrations. Dozy and Molkenboer (1854, Tab. 2 1-18); Cardot (1900, Pl. 14 62 A-C); Bartram (1949, Fig. 32 E-G); Florschutz (1964, Fig. 38 A-I); Yano (1975, Fig. 6 A-I); Delgadillo and Sharp (1976, Figs. 1-3); Griffin (1979, Figs. 63-67); Yano (1992, Fig. 27).
Habitat. Epiphytic on trees (particularly palms), shrubs, rotten wood, humus, occasionally on rock; 10-1000 m.

Distribution in Central America. BELIZE. Belize: Lundell 1497 (MO, US); Cayo: Bartlett 12030 (MO, US); Toledo: Boutin & Schlosser 5019 (MO). GUATEMALA. Alta Verapaz: Johnson 98 (US); Izabal: Steyermark 41830 (F); Jalapa: Kellerman 7394 (US); Peten: Contreras 3504 (MO). HONDURAS. Atlantida: Standley 52734 (F, US); Cortez: Standley et al. 7042 (F); Gracias a Dios: Nelson & Cruz 9297 (UNAH); Olancho: Allen 12512 (MO, TEFH); Yoro: Allen 13476 (MO, TEFH). NICARAGUA. Zelaya: Stevens 4887A (MO). COSTA RICA. Cocos Island [Puntarenas]: Gomez 18105 (MO); Heredia: Carballo 175 (MO, CR); Limon: Crosby 3684 (MO); Puntarenas: Gomez 20005 (MO). PANAMA. Bocas del Toro: Crosby 4084 (MO, PMA); Canal Area: Montalvo & D'Arcy 377 (MO); Chiriqui: Salazar et al. 9064 (PMA); Cocle: Crosby 4437 (MO, PMA); Colon: Crosby 10461 (MO, PMA); Darien: Salazar & Gradstein 9312 (PMA); Panama: Crosby 10410 (MO, PMA); Veraguas: McPherson 11378 (MO, PMA).

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Octoblepharum pulvinatum is a fairly common species in Central America. It is marked by its greenish yellow color and erect-spreading, fragile leaves. It may occur mixed with O. albidum, which differs in its generally smaller size, spreading to recurved, sturdy leaves, and 8 peristome teeth. Although in Central America O. pulvinatum is characteristically greenish yellow in color, there are a few collections that are rose-colored at base. In South America color does not appear to be a reliable feature of this species, since some collections have leaves nearly as reddish as O. cocuiense. The larger size and presence of a pseudocostal region in the leaves of O. cocuiense distinguish that species from O. pulvinatum.


Plants in dense turfs to 2 cm high; stems erect, dark red, sparingly branched, tomentose. Leaves fragile, erect, closely appressed with a metallic luster, red-purple at base, gradually changing to yellow-green above, (3.8-)5.3-7(-10.7) mm long, with broad hyaline lamina gradually narrowed to the upper leaf, apex obtuse to acuminate or cuspidate; margins entire, undulate-crenulate by enlarged bulging marginal leucocysts;
basal lamina with rectangular to hexagonal, strongly pitted leucocysts, limbidium of narrowly elongate cells in 3-5 rows, leucocysts in the lower half of the lamina with large perforations forming a conspicuous area near the costa resembling cancellinae; leaves in cross section at the apex with two layers of leucocysts on each side of the central chlorocyst layer, at middle with 3-4 layers of leucocysts on each side. Setae light brown to dark red, 6-9 mm long; capsules rounded to cylindric, erect to subinclined, orange, darker and slightly constricted under mouth, exothecial cells bulging outward at base, 1-1.8 mm long; peristome of 16 paired, elongate teeth, pale yellowish, deflexed when wet, erect when dry; opercula to 1 mm long. Calyptrae 1.7-2 mm long. Spores brown, oval triangular, 15-22.5 um in diameter.


Habitat. Epiphytic on trees and on dead logs, sand, or moist rock crevices; at low elevations to above 1000 m.

Distribution in Central America. PANAMA. Darien: McPherson 11623B (MO, PMA); Veraguas: Crosby 10257 (MO, PMA).

World range: Central America; Western and Northern South America, Brazil.

Octoblepharum stramineum is a rare species in Central America. Florschutz (1964) considered it very close to O. albidum from which it differs in its glossy reddish, erect-spreading, more or less fragile leaves. It differs also in its 16 peristome teeth, basal laminal cells with large pores, and in the basal laminal cells near the costa extensively resorbed.


Plants in dense to loose turfs, whitish green to yellowish white, to 3 cm high; stems erect, sparingly branched. Leaves flexuous, erect spreading to curved, acute to acuminate, occasionally apiculate, 5-11 mm long, plane above, concave and keeled from base to slightly above lamina; margins entire, undulate at apex, limbidia 1(-2)
cells wide at apex; basal lamina narrow, gradually tapering to the costal area, leucocysts quadrate, rectangular to irregularly hexagonal, pitted, in 1(-2) layers; ventral leucocysts at costal area long rectangular to oblong, to 245 um long, strongly pitted; cross section of leaves at apex with one layer of abaxially oriented chlorocysts surrounded dorsally by a single layer of leucocysts and mid-ventrally by two layers; at midleaf with the chlorocyst layer surrounded by 3(-4) layers of mid-ventral leucocysts and dorsally by 1-2 layers. Fusiform gemmae and rhizoids clustered at apex of leaf. [Description of sporophyte from South American material.] Setae smooth, orange-red, to 2 cm long; capsules cylindric, erect to subinclined; urn to 2 mm long, light orange at base, darker towards mouth; stomata superficial at base of urn; peristome teeth 16, pale, hyaline, with vertical and semi-circular thickenings on the dorsal plate; opercula long rostrate. Spores strongly papillose, 18-22.5 um in diameter. Calyptrae cucullate, to 2 mm (one specimen) long, orange-red above, stramineous below.

Illustrations. Gleason (1931, Pl. 45).

Habitat. On small roots and humus base of overturned trees, on branches and tree trunks, in moist soil; 2354 m.


World range: Central America; Northern South America.

Octoblepharum tatei has a soft appearance that is not found in any other Central America species of Octoblepharum. It is distinguished by its whitish green color and long, curved to erect-spreading leaves that are acute to acuminate at the apex and keeled at base. In Central America this species may be confused with O. pulvinatum or O. erectifolium. It differs from O. pulvinatum by its acute to acuminate apices with long rectangular to oblong, strongly porose cells, longer laminal cells and keeled leaves. From O. erectifolium it differs by its shorter, flexuous, sturdy leaves with long rectangular leucocysts, and laminal cells strongly and conspicuously pitted.

This species was previously known only from the Guayana Highland of Venezuela and Guyana.
Leucophanes Brid., Bryol. Univ. 1: 763. 1827.

Plants glaucous green, in dense to loose turfs; stems erect, orange-brown to dark red, sparingly branched; rhizoids papillose. Leaves erect to more or less contorted when dry, loosely overlapping when wet, narrow to broadly lanceolate, concave to keeled at base or through most of their length, plane above, acuminate, acute, obtuse, retuse or the apex bent backwards; margins serrate particularly in the upper third with single or paired teeth; basal hyaline lamina asymmetrical, extending to 1/5-1/3 length of leaf on both sides of costa (central stereid band), uni- to irregularly bistratose; costa percurrent to shortly excurrent, smooth to strongly papillose on back. Gemmae on leaf tips, papillose, oblong to clavate, 6-10-celled. Dioicous or monoicous. Setae 3.1-15 mm long, sinistrorse, smooth; capsules 1.8-3.0 mm long, dark orange, erect to horizontal; stomata superficial at capsule neck; peristome of 16, more or less papillose, lanceolate teeth, with a prostome 2-3 cells high; opercula long, subulate-rostrate. Calyptrae cucullate. Spores 10-20 um in diameter.

The leaves in Leucophanes have a chlorocyst/leucocyst structure generally associated with the Leucobryaceae. However, Edwards (1979) interpreted the Leucophanes peristome as typical for the Calymperaceae. Robinson (1985) considered the structure of the peristome a widespread by-product of an erect capsule. Nevertheless, he transferred the genus from the Leucobryaceae to the Calymperaceae on the basis of a number of gametophytic features (costal stereids, leaf shape and margin, and leucocysts with pores).

Pored leucocysts are found in a number of genera and appear to have evolved independently several times. For this reason and because the chlorocyst/leucocyst leaf structure is not otherwise found in the Calymperaceae, Leucophanes seems best treated in the Leucophanaceae along with Exodictyon and Exostratum. These three genera appear closely related to the Calymperaceae as evidenced by the gametophytic and sporophytic features cited above. Arthrocormus and Octoblepharum also appear to be near the Leucophanaceae.


Plants delicate, to 2(-4) cm. Leaves 3-5.3 mm long, loosely overlapping, slightly twisted above midleaf when dry, narrowly lanceolate, with 2-3 orange-red colored cells at insertion, apex acute, rounded obtuse, more or less truncate, emarginate, or more or less obcordate, recurved in some specimens, often gemmiferous; margins serrate at apex, entire below; costa (central stereid band) narrow, percurrent, somewhat scabrous abaxially near apex; transverse section of leaf with one layer of leucocysts on each side of the central chlorocyst layer; abaxial leucocysts in surface view quadrate to elongate rectangular, 27-63(-100) um long at midleaf. Gemmae fusiform, clavate, papillose, variable in number of cells. Dioicous. Sporophytes unknown in the Neotropics.
Illustrations. Dusen (1896, p. 15 A-I, as L. cameruniae, p. 17 A-B, as L. calymperaceum, p. 17 A-E, as L. obtusatulum, Tab. 1 39-40, 42); Florschutz (1964, Fig. 32 A-C, as L. mittenii); Salazar Allen (1986, Figs. 13-16, 18, 20, 23, 29, 48, 84-85, 252-286); Salazar Allen (1993, Fig. 1).

Habitat. Corticolous (commonly on palm trees) or occasionally on decaying wood in tropical rain forests; sea level-800 m.

Distribution in Central America. NICARAGUA. Zelaya: Proctor et al. 27185 (NY). COSTA RICA. Limon: Stevens 24278 (MO). PANAMA. Cocle: Salazar et al. 12349 (PMA); Colon: Crosby 10322 (G, MO, PMA); Darien: Salazar & Gradstein 9320 (PMA); Panama: Lara 333 (PMA); Veraguas: Crosby 10160 (MO, PMA).

World range: Central America; Caribbean, Western and Northern South America, Brazil; West, West-Central, and East Tropical Africa, Western Indian Ocean.

This species may be confused with Ochrobryum or delicate species of Syrrhopodon because of its whitish green appearance and small size, but the presence of costate leaves with multistratose lamina distinguishes it.

CALYMPERACEAE
by William D. Reese

Plants erect (rarely prostrate), with simple to highly forked stems in loose to dense tufts, mats, or cushions; stems lacking central strand; rhizoids brown to red or purple.
Leaves sometimes dimorphic (gemmiferous and nongemmiferous), straight to crispate or variously contorted or twisted when dry; intramarginal files of differentiated cells (teniolae) present (some Calymperes) or lacking (most Syrrhopodon); costa single and strong, in cross section showing median guide cells with dorsal and ventral bands of stereid cells, the latter poorly developed in some Calymperes; lower lamina mostly sheathing and with evident shoulders, usually including conspicuous fields (cancelliniae) of enlarged, hyaline, externally and internally porose cells; upper lamina shorter to many times longer than lower lamina, margins mostly variously thickened or bordered, or both, but rarely undifferentiated; cells of upper lamina isodiametric to vertically or transversely elongate, smooth to uni- or pluripapillose. Gemmae frequently present on leaves in Calymperes, less common in Syrrhopodon, mostly ventral on costa at leaf apex but sometimes along costa at midleaf or lower, clavate, fusiform, or filiform-uniseriate, leaf tips deciduous in one species. Dioicous, rarely monoicous. Perichaetial leaves scarcely differentiated. Setae smooth, mostly elongate; capsules mostly cylindric, mostly exserted, rarely immersed; stomata scanty, phaneropore; peristome single or lacking, often vestigial, the teeth variously papillose externally, smooth or papillose internally, with weak transverse bars; opercula rostrate. Calyptrae naked, smooth or papillose, cucullate (rarely campanulate) and deciduous (Syrrhopodon) or clasping the seta below the capsule and persistent (Calymperes), the spores then escaping through vertical fissures in the calyptra. Spores mostly finely papillose.

This is a mostly tropical to subtropical family with a few temperate species; most of its members are epiphytic or less commonly terrestrial. Calymperes, with eight species, and Syrrhopodon, with 24 species and varieties, occur in Central America.

Key to the Genera
1. Sporophytes present
2
1. Sporophytes lacking
3

2. Calyptra cucullate, deciduous; peristome present or lacking
2. Syrrhopodon
2. Calyptra clasping seta below capsule, persistent; peristome lacking
1. Calymperes

3. Margins of upper lamina with border of elongate hyaline cells (sometimes
2. Syrrhopodon

3. Margins of upper lamina lacking border of elongate hyaline marginal cells, variously bordered otherwise or undifferentiated

4. Teniolae present (at least in some leaves)
   1. Calymperes
   4. Teniolae lacking

5. Gemmae along ventral surface of costa at midleaf
   2. Syrrhopodon
   5. Gemmae on leaf tips only, or lacking

6. Upper lamina linear; cells mostly or in part transversely elongate
   1. Calymperes
   6. Upper lamina variously lanceolate; cells isodiametric

7. Leaf margins crenulate, unistratose; plants very small, often purplish
   Calymperes rubiginosum
   7. Leaf margins entire to serrate, mostly thickened; plants small to large, never purple
8. Leaves bearing gemmae all around apex of costa; plants minute, 2-3 mm tall
   Calymperes tenerum
8. Leaves bearing gemmae only on ventral surface of costa; plants taller than 3 mm
   2. Syrrhopodon


   Plants mostly tufted, with erect simple or forked stems. Leaves with cells of upper
   lamina isodiametric or transversely elongate; margins generally thickened but mostly
   lacking hyaline cells; teniolae. Gemma receptacles and highly modified gemmiferous
   leaves common. Capsules exserted, cylindric; peristome lacking. Calyptrae persistent,
   plicate, enclosing capsule, clasping operculum by its rostrum and twisting around seta
   below, with vertical slits above through which the spores escape.

   Eight species of Calymperes are known to occur in Central America; two others, C.
   pallidum and C. tenerum, are also treated here because they are expected to occur
   there. Most Calymperes species are corticolous, but a few grow on rocks and soil.
   Some attain modest elevations, but the majority are plants of warm, humid lowlands.
   Six of the Central American species of Calymperes occur more or less throughout the
   region, but C. nicaraguense and C. venezuelanum have more restricted distributions.

   When the capsules of Calymperes are dry, the operculum - its rostrum gripped by
   the tip of the calyptra - is held away from the mouth of the capsule, allowing the spores
   to disperse through the gaping vertical slits in the calyptra. When the capsules are moist
   the operculum is held against the mouth of the capsule - closing it - and the slits in the
   calyptra are closed.

   The sole character that distinguishes Calymperes from Syrrhopodon is the
   remarkable persistent calyptra; the two genera intergrade in all other respects. Although
   teniolae occur in some species of Syrrhopodon, the character when present is diagnostic
   for Calymperes in Central America. Calymperes is easy to recognize when sporophytes
   are present or if the leaves bear teniolae. In the absence of teniolae, sterile specimens of
   Calymperes may be difficult to distinguish from sterile plants of species of Syrrhopodon

   with unbordered leaves.
1. Upper lamina linear, its cells transversely elongate, at least in part 2
1. Upper lamina variously lanceolate, its cells isodiametric 4

2. Leaves stiff, fragile, with a petiole-like constriction between the lower and upper laminae; plants of high elevations 10. C. venezuelanum
2. Leaves soft, flexible, lacking petiole-like constrictions; plants of low elevations 3

3. Cells of upper lamina smooth dorsally and ventrally; leaves mostly more than 8 mm long 4. C. lonchophyllum
3. Cells of upper lamina papillose dorsally and ventrally; leaves mostly less than 8 mm long 3. C. levyanum

4. Distal cells of cancellinae distinctly mammillose ventrally 5
4. Distal cells of cancellinae plane ventrally 6

5. Costa in cross section with well developed ventral and dorsal bands of stereid cells 2. C. erosum
5. Costa essentially lacking stereid cells 7. C. pallidum

6. Teniolae present, sometimes weak or more or less lacking in some leaves in some plants 7
6. Teniolae lacking

7. Cancellinae forming broad angles above with costa; upper lamina mostly as wide as or wider than lower, its cells smooth or slightly bulging-mammillose ventrally; hairbrush-like tufts of gemmae commonly present ventrally on expanded gemma receptacles at leaf tips

6. C. palisotii

7. Cancellinae mostly forming acute angles above with costa; upper lamina usually narrower than lower, its cells papillose or highly mammillose ventrally, at least in upper part; gemmae present or lacking but not in hairbrush-like tufts

8. Cells of upper lamina smooth dorsally; teniolae not extending much above shoulders, often indistinct or vestigial; upper lamina more or less subulate

5. C. nicaraguense

8. Cells of upper lamina papillose dorsally; teniolae extending well above shoulders, very distinct; upper lamina lanceolate

1. C. afzelii

9. Leaf margins crenate, unistratose; plants often purplish

8. C. rubiginosum

9. Leaf margins entire to serrulate, often thickened; plants green

9. C. tenerum


Plants yellowish to dark green or brown, dull, in low, thin turfs or gregarious and tufted, mostly to 10 mm tall. Leaves 3-6 mm long, not much contorted when dry, ligulate to lanceolate from broader base; margins thickened, serrate to coarsely toothed
above; teniolae very conspicuous; cancellinae distinct, sometimes glossy and conspicuous when dry; cells at midleaf obscure, smooth or finely papillose dorsally, bulging papillose ventrally, 4-5 μm in diameter; costa smooth or papillose. Gemmiferous leaves often abruptly constricted at apex and forming a narrow "proboscis" with margins revolute around costa and bearing gemmae only on ventral surface of costa. Setae 4-5 mm long; capsules 2-2.5 mm long; opercula 0.75 mm long. Calyptrae 4 mm long. Spores 19-23 μm, finely papillose.

Illustrations. Bartram (1949, Fig. 36 A-E, as C. donnellii); Crum and Anderson (1981, Fig. 114 G-L, as C. donnellii); Florschutz (1964, Fig. 52, as C. donnellii); Reese (1961, Figs. 75-83, as C. donnellii); Reese et al. (1986, Fig. 20); Reese (1993, Fig. 59).

Habitat. On tree trunks, logs, rock, and soil; mostly at low elevations in coastal and interior forests but collected to 900 m.


NICARAGUA. Managua: Standley 8361 (F); Zelaya: Kofron 3C (LAF). COSTA RICA. Cocos Island [Puntarenas]: Gomez 4560 (MO); Puntarenas: Hammel 18334 (MO). PANAMA. Canal Area: Crosby 3937 (DUKE, LAF, MO); Colon: Crosby 4556 (MO); Darien: Allen 8733 (MO); Los Santos: McPherson 13508A (MO); Panama: Crosby 4548A (MO).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean, Western and Northern South America, Brazil; China, Eastern Asia; Indian Subcontinent, Indo-China, North Indian Ocean, Malesia; West, East, and South Tropical Africa, Western Indian Ocean; Australia; Northwestern, Southwestern, and South-Central Pacific.

This moss, formerly known in the Americas as Calymperes donnellii, has small, obscure cells, prominent teniolae, and gemmae borne ventrally on often modified leaf tips. It is similar to C. erosum, which differs in its larger leaf cells and gemmae borne all around the tip of the costa; further, the distal cells of the cancellinae in C. erosum are markedly mammillose ventrally (at least along the distal edges of cancellinae). In contrast those of C. afzelii are plane distally.

2. Calymperes erosum C. Mull., Linnaea 21: 182. 1848. Type. Suriname, Kegel

Plants yellowish green or darker, sometimes tinged below with pink or purple, to 10 mm tall, in thin to dense tufts or turfs, often glossy when dry due to exposed, refractive cancellinae. Leaves somewhat dimorphic, 3-4.5 mm long, involute and curved when dry, ligulate to lanceolate from broader base; margins thickened, serrate; teniolae conspicuous; cancellinae distinct, often glossy when dry, their ventral distal cells notably mammillose with the mammillae pointing distally (but mammillose cells sometimes restricted to distal edges of the cancellinae); cells at midleaf 5-7 | 7-10 um, papillose dorsally, mammillose-papillose ventrally; costa mostly smooth dorsally, mammillose-papillose ventrally. Gemmiferous leaves scarcely differentiated or often narrowly acuminate and reduced to naked costa distally, bearing often spherical clusters of gemmae all around on the excurrent tip of the costa. Setae 3-4.5 mm; capsules 2.5-3 mm long; opercula 0.6-0.8 mm long. Calyptrae 3.5-4.5 mm long. Spores finely and densely papillose, 20-26 um.

Illustrations. Bartram (1949, Fig. 36 I-K, as C. emersum); Crum and Anderson (1981, Fig. 114 A-F); Florschutz (1964, Fig. 50); Reese (1961, Figs. 84-93); Reese et al. (1986, Figs. 27-28); Reese (1993, Fig. 60).

Habitat. On tree trunks, logs, rocks, and soil in forests; sea level to 650 m.
2. Calymperes erosum

Distribution in Central America. BELIZE. Toledo: Davidse & Brant 31884 (MO).
COSTA RICA. Limon: Steere CR-10 (NY); Puntarenas: Gomez 20001 (MO). PANAMA. Canal Area: Willis (F, MO, PMA); Colon: Crosby 4551 (MO, PMA); Darien: Knapp & Mallet 3144 (MO); Panama: Crosby 10427 (LAF, MO).
World range: Southeastern U.S.A.; Mexico; Central America; Caribbean, Western and Northern South America, Brazil; Southeastern Europe; China; Indian Subcontinent, Indo-China, North Indian Ocean, Malesia; Macaronesia, West and South Tropical Africa, Western Indian Ocean; Australia; South-Central Pacific.

Calympere erosum is a variable species, ranging from forms with all leaves broad and vegetative to those with all leaves narrowly acuminate and gemmiferous (in some specimens the gemmae may have fallen). Although the extreme forms are very different in appearance, they are still identifiable by the ventrally mammillose distal cells of the cancellinae and the gemmae (or their vestiges) borne all around the excurrent tips of the costa. Calymperes pallidum, also with ventrally mammillose cancellinar cells, lacks costal stereids and has gemmae only ventral on the leaf tips; C. tenerum, which bears gemmae all around the tip of the excurrent costa, lacks teniolae. Calymperes afzelii does not have mammillose cancellinar cells and bears gemmae only ventrally on its leaf tips.


Plants dull green, in low, springy tangles; stems to 1.5 cm tall but commonly very short and plants appearing stemless. Leaves narrowly linear, mostly less than 8 mm long, contorted-coiled at tips when dry, more or less straight below; margins thickened, toothed or entire at shoulders, serrate above; cancellinae sharply distinct, often stoutly
bulging ventrally in distal portion; cells of upper lamina usually obscure and densely papillose, but sometimes papillae small and rather inconspicuous, cells sometimes smooth or nearly so in lower part of upper lamina, at least some cells transversely elongate, especially just above cancellineae; costa smooth. Setae 6 mm; capsules 1.8 mm long; opercula 1.7 mm long. Calyptrae roughened above. Spores 22-24 um, finely roughened.

Illustrations: Florschutz (1964, Fig. 43); Magill (1981, Fig. 44 10-18); Reese (1961, Figs. 7-10); Reese (1993, Fig. 54).

Habitat. On tree trunks and logs in forests; sea level to 350 m.


World range: Mexico; Central America; Caribbean, Northern South America, Brazil; China, Eastern Asia; Southern Africa.

Although this species is only infrequently collected, it surely has a wider range in Central America than existing specimens indicate. It often resembles a small version of Calymperes lonchophyllum, usually appearing dull because of its generally very papillose leaf cells. Some specimens, such as Allen 5532 (MO), consist of rather large plants. The leaves of occasional specimens (such as Bowers 603-a, LAF, MO, TENN) are less papillose than is typical for the species and so are more like the leaves of C. lonchophyllum. Due to its small stature C. levyanum may be overlooked in the field or disregarded as underdeveloped plants of C. lonchophyllum.


Plants dark green, in low, dull tangles and dense springy mats; stems to 20 mm tall but commonly very short and plants appearing stemless. Leaves narrowly linear, mostly to 14 mm long, variously contorted-coiled above when dry, often transversely undulate; margins heavily thickened, remotely toothed above; cancellinae sharply distinct; cells of upper lamina smooth, some or most transversely elongate, often bistratose; costa smooth. Setae 10 mm long; capsules 1.7-2.5 mm long; opercula 1.1 mm. Calyptrae 4-4.7 mm, papilllose roughened above. Spores 17-24 um, finely papillose.

Illustrations. Bartram (1949, Fig. 37 D-G); Florschutz (1964, Fig. 41); Reese (1961, Figs. 1-6); Reese (1993, Fig. 53).

Habitat. Mostly corticolous, occasionally on rock and dead wood in forests; sea level to 720 m.

Distribution in Central America. BELIZE. Belize: Gentle 898-C (LAF, NY); Cayo: Bartlett 11738 (MO); Toledo: Gentle 7625 (LAF, MO). GUATEMALA. Alta Verapaz:

Steyermark 44465 (F); Izabal: Steyermark 38891 (F); Peten: Bartlett 12441 (MO).

HONDURAS. Trumfo Lagoon, Wilson 183 (NY). NICARAGUA. Zelaya: Stevens 8547 (MO). COSTA RICA. Guanacaste: Hammel et al. 15382 (MO); Limon: Gutierrez 148 (F); Puntarenas: Liesner 1955 (MO). PANAMA. Bocas del Toro: McPherson 11443E (MO); Canal Area: Salazar & Chung 7856 p.p. (PMA); Colon: Crosby 10759 (LAF, MO, PMA); Panama: Crosby 10113 (MO); San Blas Comarca: Allen 4972A (MO); Veraguas: Crosby 10195 (MO, PMA).

World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil; China, Eastern Asia; Indian Subcontinent, Indo-China, North Indian Ocean, Malesia; West, West-Central, East, and South Tropical Africa; Australia; Southwestern Pacific.

Its linear leaves with smooth cells, commonly stemless appearance, and compact, springy habit make Calymperes lonchophyllum easy to recognize. Only C. levyanum and C. venezuelanum are similar in Central America; the papillose cells of the former and petiole-like leaf constriction of the latter differentiate them. As in C. levyanum, plants of C. lonchophyllum commonly have such short stems that the leaves seem to arise directly from the substrate.
4. Calymperes lonchophyllum  5. Calymperes nicaraguense

Calymperes heribaudii Par. & Broth., Rev. Bryol. 35: 49. 1908. Type. Panama, Helion (M, NY, REN).

Plants glossy, light green, often matted with rust-colored rhizoids below, in cushions, tufts or gregarious; stems 10-20 mm tall. Leaves subulate, mostly 4-5 mm long from broad base with conspicuously flaring shoulders, involute and curled-contorted when dry; margins thickened, finely serrate by projecting cells above, serrate at shoulders; teniolae variable, extending irregularly downward into shoulders from above or lacking; cancellinae often conspicuous and glossy when dry; cells at midleaf 8 um in diameter, mammillose ventrally, smooth or somewhat papillose dorsally; costa rough distally on dorsal surface, smooth or mammillose-papillose ventrally.
Gemmiferous leaves not much differentiated, contracted at tips and bearing gemmae on ventral surface of costa, which may be shortly excurrent. Setae 4-5 mm; capsules 2-2.5 mm long; opercula 1 mm long. Calyptrae rough above. Spores 17-30 μm, finely papillose.

Illustrations. Bartram (1949, Fig. 37 A-C); Florschutz (1964, Fig. 53); Reese (1961, Figs. 94-100); Reese (1993, Fig. 72).

Habitat. On bark, dead wood, and rocks in forest; 5-1000 m.

Distribution in Central America. BELIZE. Stann Creek: Gentle 3531 (F, LAF, NY); Toledo: Gentle 5303 (LAF, MO). GUATEMALA. The type of Calymperes carionis. HONDURAS. Olancho: Allen 12608 (MO, TEFH). NICARAGUA. Zelaya: Pipoly 3764 (MO). COSTA RICA. Alajuela: Brenes 17150 (F); Limon: Alfaro 109 (F, NY); San Jose: Skutch 2207 (MO). PANAMA. Bocas del Toro: McPherson 11443D (MO); Canal Area: Salazar & Chung 7856 p.p. (PMA); Chiriqui: Allen 5374 (MO); Darien: Allen 8951 (MO); Los Santos: Croat 34542 (MO); Panama: Crosby 4327 (MO, PMA).

World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

Calymperes nicaraguense is closely related to and often looks like C. guildingii Hook. & Grev. by its contorted-curled leaves, which are involute-subulate above the broad, flaring bases. The latter, which is not yet known from Central America, has strong, very distinct teniolae composed of sinuous, pitted, thick-walled cells in the leaf shoulders. Calymperes nicaraguense is neither common nor abundant in Central America. It differs from C. erosum, among other ways, in lacking ventrally mammillose distal cells in its cancellinae, weak variable teniolae, and in bearing gemmae only ventrally at the leaf tips; C. afzelii differs in having small obscure leaf cells and consistently strong teniolae.


Plants dark green, to 10 mm tall, in low, dense turfs or clumps. Leaves dimorphic,
involute and contorted when dry, mostly 2-3 mm long, oblong to broadly lanceolate, bases not or only somewhat broader than upper lamina (except in gemmiferous leaves); margins usually slightly thickened, entire above, more or less serrate at shoulders; teniolae usually conspicuous at shoulders and above; cancellinae distinct, often truncate distally; cells at midleaf mostly 7-8 um in diameter, smooth or slightly papillose dorsally, bulging ventrally; costa smooth except toward apex. Gemmiferous leaves narrowed distally, often terminating in a distinct expanded gemma-receptacle bearing gemmae in a hairbrush-like tuft on ventral surface. Setae 3 mm long; capsules to 2 mm long; opercula 0.5 mm long. Calyptrae 3-3.5 mm long. Spores mostly 28-35 um, finely papillose. Spores 17-24 um, papillose. Calyptrae 3.5-4 mm long, smooth or slightly roughened above.

Illustrations (all as C. richardii). Bartram (1949, Fig. 36 F-H); Crum and Anderson (1981, Fig. 115 A-G); Florschutz (1964, Fig. 49); Reese (1961, Figs. 35-43); Reese (1993, Fig. 62).

Habitat. On tree trunks, dead wood, and rocks in coastal and inland forests; at low elevations.

Distribution in Central America. BELIZE. Belize: Spellman & Stoddart B128a (MO); Orange Walk: Davidse & Brant 32732 (MO); Toledo: Gentle 7503 (LAF, MO).
HONDURAS. Colon: Saunders 913 (MO); Yoro: Allen 13465 (MO, TEFH).
NICARAGUA. Zelaya: Stevens 19995 (MO). COSTA RICA. Guanacaste: Bowers 315-a (LAF, TENN); Puntarenas: Stone (LAF). PANAMA. Bocas del Toro: Crosby 4083 (LAF, MO); Canal Area: Tyson 1177 (LAF, NY); Colon: Barsallo et al. 20 (LAF, MO, PMA); Herrera: McDaniel 8006 (NY); Panama: Crosby 4546 (MO); San Blas Comarca: Allen 4974 (MO); Veraguas: Lewis et al. 2835 (MO).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean, Western and Northern South America, Brazil; Indian Subcontinent, Indo-China; West and West-Central Tropical Africa, Western Indian Ocean.

This species was formerly known in the Americas as Calymperes richardii, a species synonymized by Edwards (1980) with C. palisotii. Although Edwards recognized the American plants as C. palisotii subsp. richardii (C. Mull.) Edwards, the
distinctions he noted between African and American specimens are minor and inconsistently present. This is a very common moss of low tropical forests and is particularly common in the coastal regions of Central America. Its broad cancellinae, often truncate distally, and common presence of hairbrush-like tufts of gemmae on gemma receptacles on the leaf tips, are distinctive.

6. Calymperes palisotii
   (Species 7, C. pallidum, is not yet known from Central America.)

   Rodriguez, Balfour (BM, lectotype, Ellis 1988).
   Calymperes uleanum Broth., Hedwigia 34: 123. 1895. Type. Brazil, Ule 1556 (H, NY).

    Plants pale, soft, yellowish green, often tinged with pink below, to 20 mm tall, leaf bases glossy and conspicuous when dry because of broadly exposed cancellinae. Leaves folded and uncinate when dry, 2-4 mm long, upper lamina linear-lanceolate, about as long as or shorter than the much broader lower lamina; margins of upper lamina slightly thickened, sharply serrate; teniolae present but sometimes obscured by
involution of leaf margins; cancellinae sharply distinct, bulging ventrally, with conspicuously mammillose cells distally on adaxial surface; cells of upper lamina smooth to papillose dorsally, highly bulging-mammillose ventrally, 6-10 um in diameter; costa usually highly papillose, lacking distinct bands of stereid cells as seen in cross section. Gemmiferous leaves not much differentiated, bearing gemmae only on ventral surface of tips. Setae 3.5 mm long; capsules 2 mm long; opercula 0.7 mm long. Spores 177-24 um, papillose.

Illustrations. Florschutz (1964, Fig. 51, as C. uleanum); Magill (1981, Fig. 45: 9-16, as C. rabenhorstii Hampe & C. Mull.); Reese (1961, Figs. 15-21, as C. uleanum); Reese et al. (1986, Figs. 29-30, as C. gemmiphyllum Fleisch.); Reese (1993, Fig. 57).

Habitat. At low altitudes on tree trunks, particularly on palms.

World range: Southeastern U.S.A.; Caribbean, Western and Northern South America, Brazil; Malesia; West, West-Central, East, and South Tropical Africa, Southern Africa, Western Indian Ocean.

This species is common in Africa but is very rare elsewhere in its range. It is best recognized by its soft texture, conspicuous cancellinae, ventrally mammillose distal cells of the cancellinae, and lack of stereid cells in the costa. Calymperes erosum is similar but has conspicuous stereid bands in the costa and gemmae borne all around the tips of the costa rather than just ventrally. This species was previously known in the Americas as C. uleanum, in Africa as C. rabenhorstii, and in Asia as C. gemmiphyllum. It occurs at low elevations, particularly on the stems of palms.

   Plants small, dark green or often purplish (brown in the herbarium), in low, dense or straggly mats; stems sometimes repent with ascending branches. Leaves crispate when dry, 1.5-2 mm long, linear to oblong-lanceolate, lacking expanded shoulders; margins unistratose, crenate by protruding cells above cancellinae; cancellinae small, distinct; cells of upper lamina evenly bulging dorsally and ventrally, rounded, 13-20 um in diameter; costa smooth. Gemmiferous leaves not much differentiated, involute above and bearing gemmae only on ventral surface of costa at apex. Setae 2-3 mm long; capsules 1.8 mm long; opercula 1 mm long. Calyptrae 2.2-2.5 mm long, roughened above. Spores 25 um, finely papillose.

   Illustrations. Crum (1952, Figs. 1-5, as Macromitrium shankii); Florschutz (1964, Fig. 44, as C. rufum Herz.); Reese (1961, Figs. 30-34, as C. rufum); Reese (1993, Fig. 73).
   Habitat. On tree trunks in humid forests at low elevations.
   Distribution in Central America. HONDURAS: Morazan: Shank (DS, FH).
   World range: Central America; Western and Northern South America, Brazil.

   Calymperes rubiginosum is easily recognized by its small size, commonly purple color, leaves with unistratose, crenate margins and large bulging cells. This species has no close relatives anywhere in the world and is oddly disjunct in Central America from its main range in South America.


   Plants small, mostly 2-3 mm tall, pale green, in loose or dense tufts and turfs. Leaves involute and slightly contorted when dry, oblong-lanceolate, 2-2.5 mm long, lacking evident shoulders; margins entire, uni- or bistratose; teniolae lacking or rarely vestigial; cancellinae distinct, small, more or less truncate distally; cells at midleaf 6-8 um in diameter, finely papillose dorsally, mammillose ventrally; costa papillose-roughened, especially distally. Gemmiferous leaves with costa ecurrent and bearing
gemmae all around at apex in conspicuous, pale golfball-like spheres. Sporophytes unknown in the Americas.

Illustrations. Crum and Anderson (1981, Fig. 115 H-K, as C. nashii); Magill (1981, Fig. 45 1-8); Reese (1961, Figs. 22-29, as C. nashii); Reese et al. (1986, Figs. 31-32); Reese (1993, Fig. 63).

Habitat. Corticolous on trunks and branches in coastal areas, often near and along ocean beaches and in mangrove swamps.

Not yet known from Central America but expected to occur there.

World range: Southeastern U.S.A.; Mexico; Caribbean, Brazil; China, Eastern Asia; Indian Subcontinent, Indo-China, North Indian Ocean, Malesia; West, West-Central, East, and South Tropical Africa, Southern Africa, Western Indian Ocean; Australia; Northwestern, North-Central, Southwestern, and South-Central Pacific.

This species was formerly known in the Americas as Calymperes nashii. Although it is widespread and common in the paleotropics, it is very rare in the Americas, where it is known from southern Florida, the Bahamas (Grand Bahama Island), Puerto Rico,
10. Calymperes venezuelanum  1. Syrrhopodon autotomaius

(Species 9, C. tenerum, is not yet known from Central America.)

Haiti, Mexico (Veracruz), and Brazil (Sa~o Paulo). It is likely to turn up in Central America and should be sought in coastal sites, especially near ports, as it is likely to have been introduced to the Americas from the paleotropics. The combination of pale golfball-like spheres of gemmae borne all around on the tips of the excurrent costa, lack of teniolae, and small rectangular cancellinae is very distinctive.

Type. Venezuela, Schomburgk (BM, H, NY).

Plants glossy, pale green above, blackish in older parts, in grass-like tufts. Leaves rigidly erect to flexuous, wiry, narrowly linear, mostly broken off at midleaf, to 25 mm long, lamina absent in small area just above cancellinae where the leaf consists only of a naked costa; margins thickened, remotely toothed above, entire to serrate or toothed at shoulders; cancellinae sharply distinct; cells of upper lamina smooth, transversely elongate, often bi- to tristratose; costa smooth. Sporophytes unknown.

Illustrations. Florschutz (1964, Fig. 42); Reese (1961, Figs. 11-14); Reese and Tan (1983, Figs. 19-26); Reese (1993, Fig. 56).

Habitat. On soil and tree trunks; 300-900 m.
Distribution in Central America. PANAMA. Panama: Allen 4927 (LAF, MO).
World range: Central America; Caribbean, Northern South America.

This rare species is known in Central America only from several collections from Panama on Cerro Jefe. It is easy to recognize by its grass-like habit, brittle leaves, and petiole-like constriction above the leaf base. Remarkably, this latter feature is shared with three unrelated paleotropical members of Calymperaceae (Reese and Tan 1983).

Plants mostly tufted or gregarious on tree trunks, logs, rock, and humus; stems erect, simple or variously branched. Leaves with cells mostly isodiametric; leaf margins mostly thickened, bordered entirely or in part by elongate hyaline cells, or unbordered; teniolae and gemma receptacles mostly lacking. Gemmiferous leaves mostly not much different from vegetative leaves. Capsules exserted (rarely immersed), mostly cylindric; peristomes mostly imperfectly developed, or lacking. Calyptrae cucullate or rarely campanulate, deciduous.

Twenty-four taxa of Syrrhopodon are known from Central America. Most are corticolous, but some grow on rotting logs, humus, rock, and soil. Although commonly the plants occur in warm, humid lowland habitats, some grow at elevations of 2000 m or more. The taxa are in general widely distributed in Central America, but a few have very restricted ranges there. Syrrhopodon autotomaius and S. theriotii are endemic to Central America.

Syrrhopodon is easy to recognize when sporophytes are present or in the case of species having leaves bordered by elongate hyaline cells. However, sterile plants lacking bordered leaves may be difficult to distinguish from sterile specimens of Calymeres whose leaves lack teniolae.

Syrrhopodon simmondsii Steere was recently identified from Panama, Barro Colorado Island, by Noris Salazar Allen (Salazar Allen & Gradstein 15126, PMA); it is otherwise known from western and northern South America. Syrrhopodon simmondsii will key to couplet 3 in key B, below. It differs from the three species keyed at couplet 3 by having straight, incompletely bordered leaves with long delicate cilia at the shoulders and sometimes further distally along the leaf margins.

1. Upper lamina of leaves lacking elongate hyaline cells on margins
   Key A

1. Upper lamina of leaves bordered entirely or in part by elongate hyaline cells (border incomplete in some taxa or lacking or nearly so on some leaves)
   Key B

   Key A. Elimbate Syrrhopodon

1. Lower lamina golden brown to reddish
   2

1. Lower lamina hyaline (sometimes yellowish in S. incompleutus)
2. Cancellinae ending far below leaf shoulders, usually fragile and eroded in mature leaves

3. Leaf tips mostly uniformly deciduous; modified gemmiferous leaves lacking
   1. S. autotomaius

3. Leaf tips intact; modified gemmiferous leaves often present
   2. S. circinatus

4. Leaves monomorphic, commonly not more than 4 mm long; margins bearing 3 or more irregular rows of teeth; capsules immersed
   3. S. cryptocarpos

4. Leaves strongly dimorphic, to 10 mm or more long; margins with at most 2 rows of teeth; capsules long-exserted
   22. S. rigidus

5. Margins of upper lamina mostly unistratose; lower lamina scarcely broader than upper lamina; costa often excurrent as a long spinose-toothed awn
   23. S. theriotii

5. Margins of upper lamina mostly conspicuously thickened from apex nearly to shoulders; lower lamina commonly conspicuously broader than upper lamina; costa never excurrent as a toothed awn
6. Margins of lower lamina at shoulders bearing sharp spreading to recurved spinose teeth; leaf cells sharply papillose dorsally at midleaf; rhizoids conspicuous, dark red to purple

   6. S. gardneri

6. Margins of lower lamina entire to serrate or dentate but lacking spinose teeth, if present, teeth not spreading-recurved; leaf cells smooth or papillose distally; rhizoids brown or purple

7. Margins of upper lamina serrate-toothed in rows, the teeth forming 3 or more irregular wings from shoulder to apex; leaf cells papillose dorsally; rhizoids purple; capsules immersed

   3. S. cryptocarpos

7. Margins of upper lamina bearing at most 2 rows of teeth; leaf cells mostly smooth dorsally (sometimes somewhat papillose); rhizoids brown to purple; capsules long-exserted

8. Margins of upper lamina bearing predominantly single teeth

   10. S. incompletus var. berteroanus

8. Margins of upper lamina bearing predominantly paired teeth

9. Shoulders of lower lamina flaring, conspicuously bordered with broad band of elongate cells

   12. S. lanceolatus

9. Shoulders of lower lamina wide but not conspicuously flaring, lacking broad marginal band of elongate cells

   9. S. incompletus var. incompletus

Key B. Limbate Syrrhopodon

1. Leaf shoulders regularly toothed or ciliate, at least on some leaves, or with regular tendency to be toothed or ciliate as evidenced by obvious denticulations

   2

2. Leaf shoulders entire but occasional teeth irregularly present in some taxa
2. Cells of upper lamina smooth dorsally  
   4. S. erubescens
2. Cells of upper lamina variously papillose dorsally
3
3. Leaves moderately flexed; shoulders irregularly toothed, some leaves with entire shoulders
   24. S. tortilis

3. Leaves mostly strongly flexed; shoulders ciliate or irregularly toothed
4
4. Leaf shoulders ciliate; leaves crowded on stems
   13. S. leprieurii
4. Leaf shoulders with small cilia or denticulations but often some or most leaves entire; leaves usually remote along stem
   19. S. prolifer var. cincinnatus
5. Leaves incompletely or irregularly bordered with elongate cells
6
5. Leaves bordered essentially all around with elongate cells
7

6. Leaf apex bluntly rounded or retuse; cells of upper lamina densely pluripapillose dorsally and ventrally; leaves ligulate, bearing gemmae at tips
   14. S. ligulatus
6. Leaf apex pointed; cells of upper lamina smooth or dorsally unipapillose; leaves lanceolate, bearing gemmae at midleaf along costa  
   16. S. parasiticus

7. Cells of upper lamina, at least in part, transversely elongate; margins of upper lamina usually coarsely toothed with large, often paired teeth  
   15. S. lycopodioides

7. Cells of upper lamina essentially isodiametric; margins of upper lamina entire or toothed with mostly single teeth  
   8

8. Cells of upper lamina essentially smooth dorsally (occasionally with low papillae)  
   9

8. Cells of upper lamina distinctly papillose dorsally  
   10

9. Leaf margins and costa conspicuously ciliate-spinose at leaf tips; cancellinae bulging ventrally at distal ends  
   11. S. isthmi

9. Leaf margins and costa entire distally or occasionally with remote denticulations; cancellinae plane distally  
   5. S. flexifolius

10. Upper lamina tightly crispate to helically twisted when dry, falcate and folded on microscope slide, often not much longer than lower lamina  
    11

10. Upper lamina straight, variously curved or flexuous, or somewhat but not tightly crispate, rarely helically twisted, mostly lying flat and not falcate-folded on microscope slide, mostly 2-many times longer than lower lamina  
    12

11. Upper lamina lanceolate-acuminate; apex coarsely toothed, acute, with a large, often reflexed, sharp apical tooth; border of elongate cells complete; costa percurrent-excurrent, its dorsal surface usually heavily spinose-toothed at apex  
    7. S. gaudichaudii

11. Upper lamina ligulate; apex blunt or retuse, without coarse teeth, lacking a large, reflexed apical tooth; border lacking, weak, or incomplete distally; costa often ending below leaf tip, its dorsal surface at apex not spinose-toothed
14. S. ligulatus

12. Costa near apex essentially smooth; gemmae ventral along costa at midleaf; margins of upper lamina uniformly toothed; upper lamina 2 times length of lower lamina

8. S. graminicola

12. Costa near apex usually very rough (papillose-spinose) dorsally and ventrally; gemmae ventral on leaf tips; margins of upper lamina toothed or entire; upper lamina to many times length of lower lamina

13

13. Leaves widely spaced along stem, conspicuously flexed at 45° or more; upper lamina attenuate, often more or less helically twisted but straight when dry, not otherwise contorted; stems often simple

19. S. prolifer var. cincinnatus

13. Leaves crowded, flexed or straight; upper lamina narrowly linear to lanceolate, rarely attenuate, straight or variously contorted when dry, rarely helically twisted; stems usually repeatedly forked

14

14. Cells of upper lamina thick-walled, more or less bulging-papillose; leaves mostly toothed only toward apex; upper lamina linear to linear-lanceolate

15

14. Cells of upper lamina flat, obscure, with low papillae, walls not usually conspicuously thickened; leaves usually toothed along margins in distal 1/2-2/3; upper lamina linear to attenuate or lanceolate

17

15. Plants rather coarse, pale green or darker, neither glaucous nor in grass-like colonies; margins of lower lamina very broad, on at least some leaves bearing a few low, stout denticulations at shoulders

24. S. tortilis
15. Plants slender, pale yellow-green, often appearing glaucous, often in grass-like colonies; margins of lower lamina entire at shoulders

16. Longest leaves 5 cm or more; leaves mostly straight, often proliferous; costa of longest leaves often showing accessory guide cells in transverse section; found mostly above 1000 m

21. S. prolifer var. tenuifolius

16. Longest leaves to 2 cm; leaves straight or flexuous, not commonly proliferous; costa lacking accessory guide cells; common and abundant from sea level to over 1000 m

20. S. prolifer var. scaber

17. Leaves usually strongly flexed at shoulders, upper lamina tapering quickly and evenly to acute apex or attenuate; cancellinae usually bulging ventrally at tips; plants often glossy, dark colored, reddish or purple, almost exclusively on rock

18. S. prolifer var. acanthoneuros

17. Leaves usually straight, not flexed, upper lamina linear to broadly linear or lanceolate, not tapering except at apex; cancellinae plane ventrally at apex, not bulging; plants mostly green, mostly on trees and logs but frequently on rock

17. S. prolifer var. prolifer


Plants dark green above, brown below, cespitose; stems 1-2 cm tall, forked or simple, mostly uncinate; rhizoids light brown, abundant and conspicuous on older parts of some plants. Leaves monomorphic, involute, linear-acuminate above slightly broader yellowish base, constricted distally at site of tip dehiscence, 6-7 mm long with tip attached, 5-6 mm long without tip, flexuous to flexuous-contorted when dry, straight,
ascending-spreading and channeled when moist; dehiscent leaf tips green, filiform, not costa-like, 2-3.5 mm | 80 um, flexuous, roughened by low teeth, in cross section slightly channeled proximally, irregularly terete and grooved distally, all cells thick-walled with large lumina, guide cells of costa only distinguishable proximally; leaf margins entire or irregularly serrate at shoulders, essentially entire distally except with low teeth near and along dehiscent tip, multistratose distally, lacking stereid cells; cancellinae yellowish, narrow, fragile, eroded in older leaves, not well-differentiated distally; cells of upper lamina at midleaf thick-walled, quadrate to rectangular, averaging 7 | 11.5 um, smooth to slightly bulging dorsally, bulging to highly mammillose ventrally. Apparently dioicous; perigonia and antheridia not seen. Setae brown, 4 mm long; urns ovoid, 1.6 mm long, emergent above perichaetial leaves, with several indistinct stomata at base; peristome lacking; opercula slenderly long-rostrate, 1.2 mm. Calyptrae smooth, 2.8 mm long. Spores yellowish, smooth, 13-15.5 um.

Illustrations. Reese (1993a, Figs. 1-10).
Habitat. On tree trunks in forests; 1100-1800 m.
World range. Central America.

Plants of Syrrhopodon autotomaius, like those of many other species of Syrrhopodon, are somewhat dicranoid in appearance. At first glance (without noticing the dehiscent leaf tips), the dark green leaves, yellowish leaf bases, and fragile cancellinae are very suggestive of S. circinatus, but—among other differences-plants of the latter often have strongly dimorphic leaves and their leaf tips are never highly modified and dehiscent. Syrrhopodon autotomaius lacks the short uniseriate leaf-tip gemmae produced by most members of the Calymperaceae but presumably propagates asexually by the fragile dehiscent leaf tips. The recent discovery of this species underscores the importance of continued biological exploration in the tropics.

Costa Rica, Pittier (NY, PC).

Plants dull, brownish green, with conspicuously glossy leaf bases, in low to tall tufts; stems to 6 cm tall but mostly shorter, not often branched; rhizoids brown. Leaves strongly dimorphic, vegetative leaves involute and mostly contorted when dry, 5-6.5 mm long, acuminate to ligulate-lanceolate, apex narrowly acute; margins thickened, coarsely toothed with paired or triple teeth; leaf bases golden brown, glossy, gradually narrowing to upper lamina; margins entire or somewhat dentate; cancellinae eroded and generally lacking entirely or in part in older leaves, confined to lower, 1/3-1/2 of leaf base; median leaf cells smooth dorsally, bulging ventrally, 9-13 um | 6-8 um. Gemmiferous leaves rarely produced, narrow, stiffly erect, sometimes reduced nearly to costa, bearing scanty pale gemmae on ventral surface of tips. Setae dark red-brown, to 13 mm long; capsules 2 mm long; peristomes lacking or rudimentary; opercula to 1.8 mm long. Calyptrae smooth, 3 mm long. Spores 16-22 um, granular to finely papillose.

Illustrations. Bartram (1949, Fig. 35 A–C, as S. bernoullii); Reese (1977, Figs. 21-24); Reese (1993, Fig. 42).

Habitat. On tree trunks and logs in forests; sea level to 2000 m, more frequent at higher elevations.

Distribution in Central America. BELIZE. Toledo: Gentle 4415 (LAF, MO).
GUATEMALA. Alta Verapaz: Turckheim 6942 (BM, H, NY, PC, S). HONDURAS. Olancho: Allen 12757 (MO). NICARAGUA. Zelaya: Danin (MO). COSTA RICA. Cocos Island [Puntarenas]: Stewart 1411 (NY); Limon: Steere CR-36 (NY); Puntarenas: Koch 5041 (LAF, NY, US); San Jose: Skutch 2764 (NY). PANAMA. Bocas del Toro: Allen 5822 (MO); Chiriqui: Croat 33481 (MO); Colon: Crosby 10473 (LAF, MO); Darien: Mori & Gentry 4371 (LAF, MO); Herrera: McPherson 10948A (MO); Los Santos: Hammel 5397 (MO); Panama: Allen 4940 (MO); Veraguas: Hammel 14278 (MO, PMA).
World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

Prior to a revision of the elimbate species of American Syrrhopodon (Reese 1977), this species was generally known as S. bernoullii, a synonym of S. incompletus var. incompletus. Syrrhopodon circinatus is distinguished from S. incompletus by the presence of colored leaf bases that have fragile, eroded cancellinae and by the

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2. Syrrhopodon circinatus

Syrrhopodon rigidus is somewhat similar but has stout, often spreading or recurved teeth on the leaf shoulders and cancellinae that extend well up the leaf bases to the shoulders. The narrow, erect gemmiferous leaves and colored leaf bases of both S. circinatus and S. rigidus give the plants a characteristic aspect quite different from that of S. incompletus. This moss is quite similar to S. autotomaius, but the latter has deciduous leaf tips.


Type. Suriname, van Beek Vollenhoven (L, NY, U).

Plants small, slender, dull, green to yellowish green, in low, thin turfs; stems to 2.5 cm tall but mostly much shorter; rhizoids purple. Leaves mostly 2.5-3.5 mm long, somewhat contorted and often secund at stem tips when dry, ligulate to elliptic or oblanceolate from a scarcely broader base, apex blunt; margins thickened, coarsely serrate-toothed in rows forming 3 or more irregular wings; cancellinae small, narrow, mostly persistent, reaching to or beyond leaf shoulders, cells of cancellinae often more
or less eroded and bearing distinctive transverse, faintly colored thickenings; median leaf cells circular to rectangular, mostly 9-14 | 5.5-8.5 um, sharply papillose dorsally, mammilllose to mammilllose-papillose ventrally. Gemmae infrequently produced, in low, dense clusters along ventral surface of costa and occasionally on the thickened leaf margins near the apex. Sporophytes immersed, inconspicuous; setae to 0.7 mm long, completely enclosed by vaginula, which extends to base of urn; capsules urceolate, to 1 mm long; peristomes fragile, teeth irregular, transversely striate-papillose, to 170 um tall; opercula rostrate to conic-rostrate, to 0.7 mm long. Calyptrae to 0.7 mm long, campanulate-conical, papillose distally, barely extending below operculum. Spores 19-24 um, smooth or granular.

Illustrations. Crum (1956, Figs. 1-6, as S. alatomarginatus Crum); Florschutz (1964, Fig. 61); Reese (1977, Figs. 44-46); Reese (1993, Fig. 50).

Habitat. On tree trunks, rotted logs, and stumps in wet forests; 700 m.


World range: Central America; Western and Northern South America, Brazil; West-Central Tropical Africa.
Syrrhopodon cryptocarpos is readily identified by its leaf shape, the triply or more winged leaf margins, the peculiar faint transverse thickenings on the cells of the cancellinae, and its immersed capsules. This species can be expected elsewhere in Central America. It may be undercollected due to its inconspicuous nature.


Plants small to medium, pale green, tinged with pink below; stems to 7 cm tall but mostly much less, not much branched; rhizoids dark purple. Leaves ligulate to lanceolate, 3-6 mm long, variably curved and contorted when dry; margins ciliate below, cilia sometimes extending nearly to leaf tip or reduced or lacking in some leaves; cancellinae distinct; median cells mostly 6-7 | 9-12 μm, dorsally smooth, ventrally bulging. Gemmae ventral on leaf tips. Setae red, 5 mm long; capsules 1 mm long; peristomes of low, blunt, imperfect teeth; opercula rostrate. Calyptrae 2 mm long. Spores not seen.

Illustrations. Crum and Steere (1957, Fig. 18, as S. borinquensis Crum and Steere); Reese (1978, Figs. 56-60); Reese (1993, Fig. 21).

Habitat. On trees in forests; 350-700 m.

Distribution in Central America. COSTA RICA. Guanacaste: Alfaro 120a (FH, MICH); Heredia: Young (LAF, UWSP); Puntarenas: Karlin 9006-0405 (NY).

PANAMA. Panama: Crosby 10425 (LAF, MO).

World range: Central America; Caribbean.

Syrrhopodon erubescens is recognized by its dorsally smooth leaf cells and usually ciliate leaf margins. This species may be confused with specimens of S. leprieurii, but that species almost always has leaf cells variously papillose dorsally. Syrrhopodon isthmi is also similar but it lacks cilia on the leaf shoulders and has distally bulging
cancellinae on the ventral surface.


Plants tufted, soft, glossy, green to yellowish green above, darker in older parts, often tinged with pink below; stems to 2 cm tall, often repent and branching; rhizoids purple-brown to reddish, sometimes conspicuous in lower parts of stems. Leaves dimorphic, 1.5-4 mm long, crispate-flexuous when dry, spreading to recurved when moist, oblong to lanceolate; margins usually bordered all around with elongate hyaline cells, mostly entire, sometimes with blunt denticulations above, hyaline border sometimes reduced or lacking distally, especially in gemmiferous leaves; cancellinae broad and distinct, distally acute, pale and conspicuously exposed when dry; median cells smooth and pellucid, in vertical files, mostly collenchymatously thickened, often porose, plane dorsally or rarely with low remote indistinct papillae, nearly plane to slightly bulging ventrally, quadrate to rectangular or rounded, mostly 10-14 | 14-17 um. Gemmiferous leaves short and broad, forming comae, sometimes deltoid, gemmae long-filamentous, borne ventrally along costa. Sporophytes unknown.

Illustrations. Reese (1981, Figs. 8-15, as S. parasiticus var. flexifolius); Reese (1993, Fig. 26).

Habitat. On tree trunks, branches, twigs, and logs in forests; to 1200 m.


World range: Central America; Northern South America, Brazil.

Syrrhopodon flexifolius is generally similar to S. parasiticus except for the very large laminal cells; for other differences see discussion under that taxon. Reese (1978) treated S. flexifolius as a synonym of S. parasiticus (following Florschutz 1964, and Tixier 1967), but later (1981) recognized it as a variety of S. parasiticus. It is restored here to the specific level based on its distinctive qualities as emphasized by discovery of new specimens additional to the type.

Plants slender to robust, in tufts and cushions, green above, brown or blackish below; rhizoids dark red to purple; stems to 4 cm tall. Leaves fragile, contorted when dry, 4-5 mm long, linear-lanceolate from a broader base; margins thickened, coarsely toothed at shoulders with sharp, spreading or ascending teeth; cancellinae distinct, sharply demarcated distally from adjacent green cells; median cells of upper lamina square, uni- or pluripapillose dorsally, mammillose-papillose ventrally, mostly 8-11 um. Gemmae apparently not produced. Setae brown, 7-9 mm long; capsules 2-2.5 mm long; peristomes of eroded fragments; opercula very slenderly rostrate, 1.5 mm long.

Calyptae 3.5 mm long, roughened at tip. Spores granular, 17-19 um.

Illustrations. Reese (1977, Figs. 51-52, as S. quintasii); Reese et al. (1986, Figs. 41-42); Reese (1993, Fig. 33).

Habitat. On trees, soil, and rock in forests; at moderate elevations.

Distribution in Central America. HONDURAS. Comayagua: Allen 13708 (MO); Olancho: Allen 12857 (MO). COSTA RICA. Heredia: Croat 35538c (MO).

World range: Mexico; Central America; Western and Northern South America, Brazil; China, Eastern Asia; Indian Subcontinent, Indo-China, Malesia; West, Northeast, West-Central, East, and South Tropical Africa, Southern Africa, Western Indian Ocean; Australia, Southwestern Pacific.

At first glance Syrrhopodon gardneri looks somewhat like S. incompletus var. incompletus, but the sharp, spreading teeth on the leaf shoulders and usually conspicuous dark red to purple rhizoids are diagnostic of the species. This species is reported here new to Central America. These specimens are the first records between Mexico and South America. This species has been known in the Americas as Syrrhopodon quintasii Broth., which is based on an African type.
6. Syrrhopodon gardneri

7. Syrrhopodon gaudichaudii


Plants in loose to dense clumps, much-branched, dark green, with lower lamina pale and conspicuous; to 1-2 cm tall but often much shorter; rhizoids purple. Leaves 3-4 mm long, ligulate-acuminate, loosely to tightly crispate or coiled when dry, characteristically folded and falcate when viewed under the microscope; margins mostly entire except at leaf tip, rarely toothed at shoulders, bordered all around with hyaline cells; cancellinae distinct, conspicuous when dry; median cells obscure, 7-10 um, bulging-papillose dorsally and ventrally. Gemmae infrequently produced, ventral on leaf tips. Setae 4-5 mm long, reddish; capsules 1.5-2 mm long; peristome teeth yellow to dark red, segmented, to 100 um tall; opercula to 1 mm long. Calyptrae 2-2.5 mm long, slightly roughened above. Spores granular, 16 um.

Illustrations. Crum and Anderson (1981, Fig. 112); Florschutz (1964, Fig. 59); Reese (1978, Figs. 12-16); Reese (1993, Fig. 13).

Habitat. On tree trunks, rotting wood, sometimes on humus, soil, or rock; sea level to 2500 m.

Distribution in Central America. BELIZE. Cayo: Allen 15251C (MO); Toledo: Davidse & Brant 31932 (MO). GUATEMALA. Baja Verapaz: Sharp 5212b (NY,
TENN); Solola: Steyermark 47400B (F). HONDURAS. Comayagua: Allen 11059 (MO); Cortes: Allen 14406 (MO, TEFH); Lempira: Allen 11870 (LAF, MO, TEFH); Ocotepeque: Allen 14528 (MO, TEFH); Olancho: Allen 12598 (MO, TEFH). COSTA RICA. Cartago: Crosby 9771 (MO); Heredia: Crosby 9713 (LAF, MO); San Jose: Bowers 233-a (LAF, TENN). PANAMA. Chiriqui: Croat & Porter 16178 (LAF, MO, PMA); Colon: Crosby 10472 (LAF, MO); Darien: Allen 8901 (MO); Panama: Allen 4922 (MO).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean, Western and Northern South America, Brazil; West-Central, East, and South Tropical Africa, Southern Africa, Western Indian Ocean; North-Central Pacific.

Syrrhopodon gaudichaudii is rather variable and in several features intergrades with the S. prolifer complex. However, most specimens of S. gaudichaudii are separated from S. prolifer by their crispate leaves with short upper laminae that are folded-falcate when moist on the microscope slide. See comments under S. ligulatus, a somewhat similar moss with conspicuous pale leaf bases and leaves crisped when dry.
8. Syrrhopodon graminicola


Plants solitary, gregarious, or tufted; stems to 1 cm tall but mostly shorter; rhizoids scanty, reddish brown; leaves dimorphic, vegetative ones acuminate to linear or broadly linear above scarcely broader base, acute, 2-3.5 mm long, crispate-contorted when dry, erect-spreading when moist, often falcate-folded on microscope slide; margins of upper lamina undulate, bordered all around, toothed in upper portion, lower lamina entire; cancellinae acute to broadly acute distally; median leaf cells isodiametric, mostly 6-10 | 7-10 um, pluripapillose dorsally and ventrally. Gemmiferous leaves oblong-acute to nearly deltoid, gemmae filamentous, borne along costa at mideleaf. [Description of sporophyte based on South American specimens:] setae reddish brown, 2-2.5 mm long; capsules ovoid-cylindric, brown, 1-1.5 mm long, set somewhat obliquely on the seta; stomata not seen; peristome teeth imperfect, with yellow-orange tips, smooth, segmented, 52-65 um tall, bases fused into pale membrane; opercula 1 mm long. Calyptrae 2.5 mm long, divided into several narrow segments from base to rostrum. Spores extremely variable in size and shape, 21-47 um, spherical to ellipsoidal, dark green, finely granular, some small, colorless, empty, and collapsed.

Illustrations. Florschutz (1964, Fig. 58 i-j, as S. parasiticus var. disciformis); Reese (1978, Figs. 32-34, as S. parasiticus var. disciformis) Reese (1993, Fig. 28).

Habitat. On tree trunks and twigs.


World range: Central America; Caribbean, Western and Northern South America,
Brazil.

Plants of this species are generally similar to those of Syrrhopodon parasiticus but differ consistently in having pluripapillose leaf cells and leaves bordered all around with hyaline cells with the margins toothed distally. Further, the leaf margins tend to be undulate when dry (which can be seen under the dissecting microscope), a condition not known in S. parasiticus, where the margins are plane. This species has most recently been known in the Americas as Syrrhopodon parasiticus var. disciformis (Florschutz 1964; Reese 1978), but it merits recognition at the specific level, in which case S. graminicola is the oldest name available in Syrrhopodon. It is known in Central America from only a few specimens.

Calymperes meyeri Reese, Bryologist 60: 336. 1957. Type. Panama, Meyer 7 (TENN).

Plants dark green to brownish, tufted or gregarious; stems to 2-3 cm tall but often much shorter, often freely forked; rhizoids brown to purple. Leaves basically monomorphic, lanceolate to linear-lanceolate or nearly subulate from broad, clasping base, 4-8 mm long, variously curved-contorted to straight and appressed when dry; margins thickened, with mostly paired teeth above; leaf shoulders often with intramarginal teniola-like features; cancellinae persistent, hyaline (rarely yellowish); cells of upper lamina obscure, quadrate to elliptical, mostly 5-7 | 5-12 um, smooth or somewhat papillose dorsally, bulging ventrally. Gemmae ventral on costa at leaf tips. Setae yellowish brown, 7-12 mm long; capsules 1.5-2.5 mm long; peristomes lacking or rudimentary, consisting of fragile, eroded teeth with only a few segments; opercula slenderly long-rostrate. Calyptrae 2.5-3.5 mm long, smooth. Spores 14-19 um, nearly smooth to finely roughened.

Illustrations. Bartram (1949, Fig. 34 G-I); Crum and Anderson (1981, Fig. 109); Crum and Steere (1957, Fig. 17a); Florschutz (1964, Fig. 62 i-j); Reese (1977, Figs. 1-4); Reese (1993, Fig. 34).

Habitat. On tree trunks, logs, and humus, especially common on palm stems, in forests; sea level to 1700 m, especially common at lower elevations.
Distribution in Central America. BELIZE. Belize: Gentle 113 (MICH); Cayo: Bartlett 12085 (F, MO); Corozal: Davidse & Brant 32558 (MO); Stann Creek: Schipp 8120 (F); Toledo: Gentle 7476 (LAF, MO). GUATEMALA. Baja Verapaz: Sharp 5212 (NY, TENN); Peten: Bartlett 12250 (F, MO). HONDURAS. Atlantida: Standley 7806 (F); Colon: Saunders 789A (MO); Santa Barbara: Standley & Lindelie 7359 (F); Yoro: Allen 13592 (MO, TEFH). NICARAGUA. Zelaya: La Rue (NY). COSTA RICA. Alajuela: Brenes (F); Guanacaste: Lankester (F); Heredia: Grayum 9632 (MO); Limon: Steere CR-120 (LAF, NY); Puntarenas: Gomez 10904 (MO). PANAMA. Canal Area: Crosby 3938 (LAF, MO, PMA); Colon: Crosby 4459 (MO); Darien: Gentry M-1 (LAF, MO, PMA); Herrera: McPherson 10271A (MO); Los Santos: Stern et al. 1911 (MO); Panama: Croat 34623 (LAF, MO); San Blas Comarca: Allen 4962 (MO); Veraguas: Antonio 2352 (MO).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean, Western, Northern, and Southern South America, Brazil; West-Central and East Tropical Africa.

The plants of this weedy moss are dimorphic and occur in strict- and flexuous-leaved forms that may appear strikingly different from one another. However, under the microscope the leaves of the two forms are indistinguishable. Occasionally the leaf bases of both forms bear teniola-like features at the shoulders. The variety incompletus differs from var. berteroanus in having mostly paired teeth on the upper margins and in the upper lamina usually lanceolate rather than commonly subulate; it differs from S. circinatus and S. rigidus, among other ways, in its monomorphic leaves and persistent hyaline (but sometimes yellowish) cancellinae. Syrrhopodon gardneri is superficially similar but differs prominently in having sharp, spreading teeth at the leaf shoulders, dark red rhizoids, and strongly papillose leaf cells.

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10. Syrrhopodon incompletus var. berteroanus    11. Syrrhopodon isthmi


   Plants dimorphic, with strict- and flexuous-leaved forms, differing from var. incompletus primarily in mostly narrower, commonly subulate, leaves with markedly broadly flaring bases, with single rather than paired marginal teeth on the upper lamina; the margins of the upper lamina sometimes unistratose in part.

   Illustrations. Reese (1977, Figs. 8-10); Reese (1993, Fig. 36).
   Habitat. On tree trunks and logs in forests; 18-1700 m, but more abundant at higher elevations.

   Distribution in Central America. BELIZE. Cayo: Allen 15255 (MO); Stann Creek: Gentle 3279 (F, LAF, NY); Toledo: Allen 15419 (MO). GUATEMALA. Izabal: Standley 72778 (F, MICH, NY). HONDURAS. Olancho: Allen 12875 (MO).
   NICARAGUA. Río San Juan: Stevens 23461 (MO); Zelaya: Stevens 4888 (MO).
   COSTA RICA. Cocos Island [Puntarenas]: Gomez 18103 (MO); Alajuela: Croat 36315 (LAF, MO); Cartago: Crosby & Crosby 6081, 6321 (MO); Heredia: Young (LAF, UWSP); Limon: Stevens 23744 (LAF, MO); Puntarenas: Crosby 3711 (LAF, MO); San Jose: Standley 37836 (NY). PANAMA. Bocas del Toro: Allen 5100A (MO); Chiriqui: Allen 5492 (MO); Cocle: Crosby 4441 (F, MO); Colon: Dressler & Lewis 3742 (MO, PMA); Darien: Allen 8897 (MO); Herrera: McPherson 10350 (MO);
Panama: Crosby 10910; San Blas Comarca: Allen 4979, 4985 (MO); Veraguas: Crosby 10281 (LAF, MO).

World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

Although generally similar to the typical variety, var. berteroanus is distinguishable by the presence of single teeth on the upper leaf margins. Like var. incompletus, its leaves often bear teniola-like features at the shoulders. Typical, well-developed plants of this moss are large and often glossy and commonly have subulate leaves. Some collections of this variety have paired marginal teeth here and there, indicating intergradation with the variety incompletus.


Plants robust, pink-tinged below, branched, more or less pendent; stems to 5 cm tall; rhizoids violet-purple. Leaves acuminate above broad shoulders, 5-6 mm long, flexuous-spreading and tubulose when dry; margins narrowly bordered all around with hyaline cells, conspicuously ciliate-spinose toward leaf tip, entire below; cancellinae distinct, ventrally bulging at tips; median cells 5-7 | 12-16 um, smooth dorsally, bulging ventrally. Gemmae in tight clusters at leaf tips. Sporophytes unknown.

Illustrations. Reese (1982, Figs. 1-10); Reese (1993, Fig. 19).

Habitat. On tree in forest.

Distribution in Central America. PANAMA. Panama: Crosby 4532 (MO, PMA).

World range: Central America; Western South America.

This species, known in Central America only from the original collection, has recently been collected in the Choco region of Colombia. Although superficially similar to S. leprieurii and S. erubescens, it differs, among other ways, in having entire margins at the leaf shoulders and ventrally bulging cancellinae.
12. *Syrrhopodon lanceolatus* (Hampe) Reese, comb. nov.

Plants dark to brownish green, in low tufts; stems to 15 mm tall, simple, curved to uncinate at tips; rhizoids brown. Leaves somewhat dimorphic, straight and appressed when dry, ascending when wet, mostly 4-5 mm long, linear-lanceolate above flaring shoulders, gemmiferous leaves narrower distally than vegetative leaves; margins thickened, doubly toothed distally; cancellinae persistent, broad, rounded distally, extending well up in leaf base; median leaf cells rounded-rectangular, smooth to bulging dorsally and ventrally, 5-8 | 8-16 um. Gemmae frequent, clavate, on ventral surface of often excurrent costa at leaf tips. Setae 6 mm long, brown; capsule 2 mm long; peristome teeth pale, blunt, connivent, imperfect, segmented, to 80 um; operculum rostrate, 1 mm long. Calyptrae not known. Spores granular, to 23 um.

Illustrations. Florschutz (1964, Fig. 46, as *Calymperes lanceolatum*); Reese (1961, Figs. 52-58, as *Calymperes lanceolatum*); Reese (1977, Figs. 15-16, as *Syrrhopodon incompletus* var. *lanceolatus*); Reese (1993, Fig. 38, as *Syrrhopodon incompletus* var. *lanceolatus*).

Habitat. Dense to thin tufts on tree trunks and branches in forests; sea level to 1100-1800 m.


World Range: Central America; Western and Northern South America, Brazil.

This is the first report of *Syrrhopodon lanceolatus* for Central America. The Honduran collection site is approximately 2500 km northwest of the nearest previously known station for the species in Amazonas, Colombia. This discovery prompted a reevaluation of the taxonomic status of this moss, which is here recognized at the specific level.
This rare moss has slender, terete, uncinate-curved stems with narrow appressed leaves. To the naked eye the plants look like strict-leaved forms of *S. incompletus*, but under the microscope the very narrowly linear-lanceolate leaves with broad marginal bands of elongate cells at the flaring leaf shoulders are distinctive. No other Central American member of the Calymperaceae has this combination of characteristics. Forms of *S. incompletus* var. *incompletus* and var. *berteroanus* may have intramarginal teiola-like features at the leaf shoulders but never broad marginal bands of elongate cells. The Honduran specimen is sterile; description of the sporophyte is based on a specimen from French Guiana.

12. *Syrrhopodon lanceolatus*  
13. *Syrrhopodon leprieurii*

Plants small to robust, pale yellowish green or darker, often appearing glaucous, tinged with pink below; stems to 5 cm tall, branched, sometimes repent; rhizoids scanty, purple. Leaves flexed at shoulders, only a little curved or flexuous when dry, 3-5 mm long, tubulose above wet and dry, acuminate to acute or broadly acute, apex
spinose; margins entire to spinose-toothed above shoulders, usually strongly ciliate at shoulders but merely denticulate in some specimens; cancellinae distinct; median cells very thick-walled, mostly 5-8 | 9-12 um, nearly smooth to minutely pluripapillose to long-spinose unipapillose dorsally, highly mammillose to remarkably spinose-unipapillose or pluripapillose ventrally. Gemmae not seen. Setae red, 6-10 mm long; capsules 1.5-2.2 mm long; peristome teeth slender, pale, pointed, papillose, to 250 um tall; opercula 1-1.2 mm long. Calyptrae 2-2.5 mm long. Spores 14 um, granular.

Illustrations. Bartram (1928, Fig. 13, as S. cristatus); Florschutz (1964, Fig. 55); Reese (1978, Figs. 21-25); Reese (1993, Fig. 18).

Habitat. On humus, trees, rotting logs, and moist rock; from sea level to 2400 m, most frequent at higher elevations.

Distribution in Central America. HONDURAS. Comayagua: Allen 13815 (MO, TEFH); Cortes: Allen 14158 (MO, TEFH); Morazan: Allen 12041 (MO, TEFH); Ocotepaque: Allen 14542 (MO, TEFH); Yoro: Allen 13477 (MO, TEFH). COSTA RICA. Alajuela: Crosby 10019 (LAF, MO); Limon: Crosby 3651 (MO); Puntarenas: Hammel et al. 17854 p.p. (MO); San Jose: Crosby 10872 (LAF, MO). PANAMA. Bocas del Toro: Allen 5726 (MO); Chiriqui: Allen 5516 (MO); Darien: Allen 8854 (MO); Panama: Crosby 10047 (LAF, MO); Veraguas: Mori & Kallunki 5296 (LAF, MO, PMA).

Plants very small, in compact sods, pale green, with conspicuous leaf bases; stems mostly less than 1 cm tall; rhizoids dark red. Leaves to 2 mm long, tightly crisped when dry, often folded-falcate on the microscope slide, upper lamina lingulate, rounded to retuse at apex; margins crenate by projecting cells, border of hyaline cells usually present on at least some leaves at and just above shoulders, rarely extending beyond midleaf or lacking; cancellinae distinct; median cells obscure, quadrate, mostly 7 um, pluripapillose dorsally and ventrally. Gemmae borne ventrally along costa toward apex. Rarely fertile. Setae yellowish red, 3-4 mm long; capsules 1 mm long; peristomes fragile, irregular, teeth blunt; opercula 1 mm long. Calyptrae 2 mm long, rough above. Spores 17-19 um, granular.

Illustrations. Bartram (1949, Fig. 31 E-F); Crum and Anderson (1981, Fig. 110 H-K); Crum and Steere (1957, Fig. 17b); Florschutz (1964, Fig. 57); Reese (1978, Figs. 17-20); Reese (1993, Fig. 16).

Habitat. On bark, rotting wood, rarely rock; from sea level to 1200 m.
Distribution in Central America. GUATEMALA. Baja Verapaz: Sharp 2704 (MICH, TENN).
COSTA RICA. Cartago: Hoshizaki 598-c (LAF, TENN). PANAMA. Panama: Dodge et al. 16917a (MO).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean, Western, Northern, and Southern South America, Brazil.

The tightly crisped (when dry), lingulate leaves with bluntly rounded, sometimes retuse, apices, and the lack of a strong border of elongate hyaline cells on the upper lamina mark this moss. Small plants of Syrrhopodon gaudichaudii may closely resemble S. ligulatus at first glance but differ, among other ways, in the leaves completely bordered with hyaline cells and with a sharp apical tooth at the leaf tip. In spite of its wide range this moss is very rare in Central America.


Plants robust, yellowish green above, darker below, in dense, spreading clumps or pendent, branched; stems to 15 cm tall; rhizoids scanty, brown. Leaves linear to linear-lanceolate from a scarcely broader base, 7-10 mm long, spreading to erect-appressed when dry; margins prominently bordered by elongate cells, coarsely toothed above, at leaf base usually bordered by several to many rows of elongate, hyaline, porose cells; cancellinae distinct, supra- and paracancellinar cells usually with heavily thickened, porose walls; median leaf cells mostly square but sometimes some or all transversely elongate, mostly 12-15 um, bulging mammillose-papillose dorsally and ventrally or nearly smooth. Gemmae infrequent, brown, filamentous, on ventral (and often dorsal) surfaces of costa from tips nearly to shoulders, or restricted to distal portion of costa. Setae dark, 10-11 mm long; capsules 3-4 mm long; peristomes of fragile, imperfect teeth scarcely projecting above rim of capsule mouth; opercula 1.5-2 mm long. Calyptrae 2-3 mm long, smooth. Spores granular, 20 um.
Illustrations. Bartram (1949, Fig. 31 G-H); Reese (1978, Figs. 61-64); Reese (1993, Fig. 32).

Habitat. On tree trunks and bases, rotting wood, rocks, and soil in wet montane forests; 150-3000 m, but uncommon below 1000 m.

Distribution in Central America. BELIZE. Toledo: Allen 15381 (MO).
GUATEMALA. Baja Verapaz: Sharp 2760 (MICH, TENN). HONDURAS. Comayagua: Allen 11070 (MO); Cortes: Allen 14256 (MO, TEFH); Lempira: Allen 12234 (MO, TEFH); Ocotepeque: Allen 14468 (MO, TEFH); Olancho: Allen 12654 (MO); Santa Barbara: Allen 11613 (MO, TEFH). COSTA RICA. Alajuela: Crosby 9995 (LAF, MO); Heredia: Crosby & Crosby 6572 (LAF, MO); Limon: Gutierrez 192 (F, NY); Puntarenas: Crosby 2663 (LAF, MO); San Jose: Crosby 9724 (LAF, MO). PANAMA. Bocas del Toro: Allen 5694 (MO); Chiriqui: Allen 5498 (MO); Cocle: Croat 37465A (MO); Colon: Crosby 10459 (MO); Darien: McPherson 7003A (MO); Panama: Crosby 10054 (LAF, MO); Veraguas: Crosby 10279 (LAF, MO).

World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

Syrrhopodon lycopodioides is distinctly marked by its long, narrow, prominently toothed and heavily bordered leaves. It has no close relatives anywhere in the world and cannot be confused with any other species of Syrrhopodon.


Plants dark green, solitary, in clusters of a few, or gregarious; stems to 2 cm tall but mostly much shorter, not much forked; rhizoids brown. Leaves involute and incurved when dry, basically dimorphic, to 5 mm or more long, vegetative ones lingulate-lanceolate, propaguliferous ones broadly lanceolate to triangular and clustered at stem tips; margins mostly bordered at least in part with elongate, hyaline cells, rarely unbordered; cancellinae distinct, distally acute; median cells 7 um, smooth to
unipapillose dorsally and ventrally. Gemmae filamentous, borne ventrally along costa

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16. Syrrhopodon parasiticus 17. Syrrhopodon prolifer var. prolifer

from near cancellinae to leaf tip. Setae reddish, 3-4 mm long; capsules 1-2 mm long; peristome teeth irregular, blunt; opercula 1 mm long. Calyptrae 3 mm long. Spores 24-36 um, irregular in shape, granular.

Illustrations. Bartram (1949, Fig. 35 D-G); Crum and Anderson (1981, Fig. 113); Crum and Steere (1957, Fig. 17c); Florschutz (1964, Fig. 58 a-h); Reese (1978, Figs. 28-31); Reese (1993, Fig. 25).

Habitat. On twigs, branches, trunks, and leaves in forests; to 1600 m, but most frequent at lower elevations.

Distribution in Central America. BELIZE. Cayo: Mains 3645 (MICH).
GUATEMALA. Alta Verapaz: Standley 90775a (F); Peten: Lundell 4455 (MICH).
HONDURAS. Atlantida: Crosby 4089 (MO); Comayagua: Crosby 2801 (MO); Yoro: Allen 13586A (MO, TEFH). NICARAGUA. Zelaya: Stevens 6329 (MO). COSTA RICA. Alajuela: Crosby 10032 (MO); Cartago: Crosby 3816 (MO, NY); Limon: Gutierrez 151 (F); San Jose: Crosby 2595 (MO). PANAMA. Bocas del Toro: Allen 5238 (MO); Canal Area: Dodge & Steyermark 17046a (MO); Chiriqui: Corman 3014a (F); Cocle: Tyson & Godfrey 2476a (LAF, NY); Darien: Allen 8958 (MO); Los Santos: McPherson 13508B (MO); Panama: Crosby 10067 (LAF, MO).

World range: South-Central and Southeastern U.S.A.; Mexico; Central America; Caribbean, Western, Northern, and Southern South America, Brazil; China; Indo-
China, Malesia; West, West-Central, and East Tropical Africa, Western Indian Ocean; Australia; Southwestern Pacific.

This is a well-marked taxon recognized by its very acute cancellinae, leaf cells smooth or sharply unipapillose, dimorphic leaves with filamentous gemmae on the larger ones, and often incomplete border of hyaline cells, which may be completely lacking in some leaves. The broad gemmiferous leaves often form distinctive comae at the stem tips. Syrrhopodon graminicola is similar but has pluripapillose cells and a complete border, which is toothed distally; S. flexifolius is also similar but has a pinkish tinge below, usually completely bordered leaves, and much larger leaf cells that are never distinctly papillose dorsally, although low remote indistinct dorsal papillae are rarely present, as in Allen 8903 (MO).

Type. Brazil, Beyrich (BM, GOET, JE, NY).

Plants pale to dark green, in loose to dense clumps; stems usually much-forked, to 1-7 cm tall; rhizoids red to brownish. Leaves to 1 cm long, straight or contorted when dry, linear to narrowly lanceolate from a scarcely broader base; margins bordered all around with hyaline cells, entire below, variously toothed above; cancellinae very distinct; median cells of upper lamina obscure, not bulging, densely pluripapillose with low papillae on both surfaces, quadrate to rectangular, mostly 5 | 5-12 μm. Gemmae not common, on ventral surface of leaf tip. Setae reddish, 5-12 mm long; capsules 1-2 mm long; peristomes of fragile, often imperfect, blunt or pointed, granular-papillose teeth to 190 μm long; opercula 1 mm long. Calyptrae 1.5-3 mm long. Spores 9-12 μm, granular.

Illustrations. Florschutz (1964, Fig. 60); Reese (1978, Figs. 1-3); Reese (1993, Fig. 1).

Habitat. On tree trunks and bases, roots, stumps, and humus, in forests; sea level to 2000 m.
Distribution in Central America. GUATEMALA. Solola: Steyermark 47986a (F).
COSTA RICA. Alajuela: Brenes (F); Limon: Steere CR-125 (NY); Puntarenas: Bowers 517-f (LAF, TENN); San Jose: Crosby & Crosby 6373B (LAF, MO). PANAMA.
Bocas del Toro: Allen 5130 (MO); Chiriqui: Crosby 3990 (MO, PMA); Cocle: Crosby 4431 (MO, PMA); Colon: Crosby 10365 (LAF, MO); Darien: Allen 8900 (MO); Panama: Allen 9046 (MO); Veraguas: Crosby 10814 (LAF, MO, PMA).
World range: Mexico; Central America; Caribbean, Western, Northern, and Southern South America, Brazil; Indian Subcontinent; East Tropical Africa, Western Indian Ocean; Australia; North Central Pacific; Subantarctic Islands.

The variety prolifer is quite variable in size of plants and shape and length of leaves, and grades into variety tenuifolius; however, the linear leaves and small, obscure leaf cells that are densely papillose with low papillae will, in most cases, identify it easily. In the very common variety scaber, also with linear leaves, the leaf cells are distinct and highly bulging-pluripapillose on both surfaces, and in varieties cincinnatus and acanthoneuros the leaves are acuminate. See Orban and Reese (1990) for a review of the S. prolifer complex.


Plants generally similar to those of var. prolifer, usually of a darker color. Leaves mostly strongly flexed at the shoulders; upper laminae tapering or attenuate; leaf cells with low papillae, as in var. prolifer.

Illustrations. Reese (1978, Figs. 7-8); Reese (1993, Fig. 3).
Habitat. Almost exclusively on rock, but sometimes on tree trunks, logs, and soil in forests; near sea level to 1700 m.
Distribution in Central America. GUATEMALA. Baja Verapaz: Sharp 5203 (NY, TENN). COSTA RICA. Alajuela: Brenes 17130 (F, NY); San Jose: Skutch 2888 (NY).
World range: Central America; Caribbean, Western and Northern South America,
Plants of variety acanthoneuros are generally similar to those of variety prolifer but differ in having the leaves usually strongly flexed at the shoulders and in their usually dark color and tapering to attenuate leaves. The leaf cells have low papillae as in variety prolifer.

18. Syrrhopodon prolifer var. acanthoneuros 19. Syrrhopodon prolifer var. cincinnatus


Plants generally soft and silky in appearance; rhizoids purple to violet; stems elongate, commonly simple. Leaves flexed, often rather far apart along the stem; upper lamina attenuate, often helically twisted; margins usually very heavily bordered, often
with toothed leaf shoulders.

**Illustrations.** Reese (1978, Figs. 10-11); Reese (1993, Fig. 5).

**Habitat.** On rotted wood, trees, and rock in forests at moderate elevations; to 1400 m.

**Distribution in Central America.** BELIZE. Toledo: Davidse & Brant 31891 (MO). HONDURAS. Comayagua: Allen 13784 (MO, TEFH); Cortes: Allen 14339 (MO, TEFH); Olancho: Allen 12506 (MO, TEFH). NICARAGUA. Granada: Croat 39148 (MO). COSTA RICA. Cartago: Crosby & Crosby 6076 (MO). PANAMA. Bocas del Toro: Allen 5685 (MO); Chiriqui: Allen 5478 (LAF, MO); Cocle: Crosby 4434 (MO, PMA); Panama: Crosby 4523 (MO, PMA).

**World range:** Central America; Caribbean, Western and Northern South America, Brazil.

The variety cincinnatus is usually easy to recognize by the characteristics noted above.


**Illustrations.** Crum and Anderson (1981, Fig. 111, as S. prolifer); Reese (1978, Figs. 4-6, as S. prolifer var. papillosus); Reese (1993, Fig. 2).


Plants commonly yellowish green, often in low grass-like tufts. Leaves linear, not or only slightly contorted when dry; median leaf cells distinct, highly bulging-papillose dorsally and ventrally.

**Illustrations.** Crum and Anderson (1981, Fig. 111, as S. prolifer); Reese (1978, Figs. 4-6, as S. prolifer var. papillosus); Reese (1993, Fig. 2).
20. Syrrhopodon prolifer var. scaber

Habitat. On tree trunks and bases, stumps, logs, humus, and soil in forests; sea level to 2000 m.


NICARAGUA. Zelaya: Stevens 18722 (MO). COSTA RICA. Alajuela: Crosby 10007 (LAF, MO); Cartago: Crosby & Crosby 6185 (MO); Heredia: Crosby 9922 (LAF, MO); San Jose: Crosby 9669 (LAF, MO). PANAMA. Bocas del Toro: Allen 5274 (MO); Chiriqui: Antonio 4112B (MO); Cocle: Antonio 3566 (MO); Colon: Crosby 10367 (LAF, MO, PMA); Darien: Allen 8858 (MO); Panama: Crosby 10047 (LAF, MO).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

The variety scaber is a weedy moss in much of its range. Its generally straight leaves when dry and distinctive highly bulging-papillose leaf cells distinguish it from var. prolifer. Like variety prolifer, this taxon grades into the variety tenuifolius. In a revision of the limbate taxa of Syrrhopodon, Reese (1978) incorrectly designated this taxon as var. papillosus (C. Mull.) Reese.

Leaves extremely long, to 5.5 cm, often with accessory guide cells in the costa (as seen in cross section), often proliferous at their tips; median leaf cells mostly like those of the variety scaber but in some specimens like those of variety prolifer; in some specimens leaves of both types may be present.

Illustrations. Reese (1978, Fig. 9); Reese (1993, Fig. 4).

Habitat. On trees, stumps, logs, soil, and humus in forests; to 2300 m, mostly above 1000 m.

Distribution in Central America. BELIZE. Cayo: Mains 3976 (MICH); Toledo: Davidse & Brant 32095 (MO). NICARAGUA. Rivas: Stevens 6546 (MO). COSTA RICA. Alajuela: Crosby 9985 (LAF, MO); Cartago: Crosby & Crosby 6317 (LAF, MO); Guanacaste: Herrera 1415 (MO); Puntarenas: Crosby 9962 (LAF, MO); San Jose: Crosby 9677 (MO). PANAMA. Bocas del Toro: Allen 5181b (LAF, MO); Chiriqui: Corman 3173 (F); Darien: Mori & Gentry 4322 (LAF, MO); Panama: Tyson 2486 (NY); Veraguas: Crosby 10297 (LAF, MO).

World range: Central America; Caribbean, Western and Northern South America, Brazil.

Plants of variety *tenuifolius* are similar in most respects to those of varieties prolifer and scaber. Only the presence of greatly elongated upper leaves and accessory guide cells in the costa distinguish the variety *tenuifolius*. The leaves of this moss rank among the longest known for any moss in the world. The longest moss leaves in the world may be those of the Asian-Oceanian *Syrrhopodon loreus* (Sande Lac.) Reese, which reach 6 cm in length (Reese et al. 1986).


Plants green to brownish green, often glossy, in dense wiry tufts and cushions, with
conspicuous, glossy, golden reddish leaf bases; stems mostly to 1 cm tall, forked; rhizoids red, conspicuous. Leaves strongly dimorphic, the narrow gemmiferous ones rigidly erect, often overtopping the broader, flexuous vegetative leaves, the latter mostly 7-11 mm long, linear or wider from a scarcely broader base; apex blunt or acute with costa sometimes excurrent; margins thickened, coarsely toothed above, basal margins usually bordered by several rows of elongate, thick-walled, more or less porose cells and with irregular, coarse, sharp teeth at least some of which are spreading or recurved; cancellinae more or less persistent, narrow, extending to leaf shoulders, distal cells often colored; median leaf cells usually incrassate, often with sinuose-porose walls, circular to rectangular, bulging ventrally, smooth or papillose dorsally. Gemmiferous leaves commonly present, reduced to naked (or nearly so) costa with vestigial laminae at base, gemmae borne on tips. Setae red-brown, 15-20 mm long; capsules ovoid, 1.5-2 mm long; peristomes lacking; opercula 2 mm long. Calyptrae 3.5-4 mm long, smooth. Spores 21-27 um, granular.

Illustrations. Florschutz (1964, Fig. 63); Reese (1977, Figs. 42-43); Reese (1993, Fig. 45).

Habitat. On tree trunks, lianas, roots, logs, soil, and rock, in moist to mesic forests; near sea level to 2100 m, most frequent above 300 m.

Distribution in Central America. COSTA RICA. Puntarenas: Crosby 3714 (MO). PANAMA. Bocas del Toro: McPherson 11409A (MO); Cocle: Crosby 4425 (MO, PMA); Colon: Hammel 3131 (MO); Darien: Folsom 6409 (LAF, MO); Panama: Allen 9049 (LAF, MO, NY, US); Veraguas: Crosby 10816 (LAF, MO, PMA).

World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

This moss is somewhat similar to Syrrhopodon circinatus, a species also having colored leaf bases. It is distinguished by its mostly linear leaves, more persistent cancellinae that extend to the leaf shoulders, bordered lower laminal margins that have coarse, sharp, often recurved teeth, and the common presence of the remarkably modified gemmiferous leaves. Gemmiferous leaves are often lacking in S. circinatus. In S. circinatus the leaf shoulders are irregularly dentate-serrate but never have sharp
spreading-recurved teeth, and the cancellinae are always eroded and confined to the lower half of the leaf base. Erect narrow gemmiferous leaves also occur in S. circinatus but are neither as common nor as conspicuous as those of S. rigidus.

22. Syrrhopodon rigidus              23. Syrrhopodon theriotii


Plants yellowish green, slender, to 8 cm tall, freely forked; rhizoids inconspicuous, yellowish brown. Leaves fragile, loosely flexuous-spreading, to 15-20 mm long, long linear-acuminate from a scarcely broader base, reduced to narrow wings along costa distally, apex often consisting of excurrent, spinose-toothed costa; margins sharply serrate at shoulders, irregularly toothed above, mostly unistratose but slightly thickened here and there, especially distally; cancellinae broad, persistent, extending to or beyond leaf shoulders; median leaf cells thick-walled, square to rectangular, 8.5-13 | 7-8.5
um, smooth, bulging or bluntly papillose dorsally, strongly bulging ventrally. Gemmae
unknown. Sporophytes unknown.

Illustrations. Bartram (1928, Fig. 14); Reese (1977, Figs. 47-50); Reese (1993,
Fig. 48).

Habitat. On trees, logs, and stumps; 1200-2400 m.

Distribution in Central America. COSTA RICA. Heredia: Croat 36060 (LAF,
MO); San Jose: Crosby 10925 (LAF, MO).

World range: Central America.

The long, slender leaves with mostly unistratose margins, narrow leaf base, and
often conspicuously excurrent costa, mark this rare endemic. The narrow leaves are
fragile and many are broken in most specimens.


Plants coarse, pale green to darker, in dense, sometimes wiry clumps; stems to 1-2

cm tall; rhizoids purple. Leaves 4-5(-7) mm long, crowded at stem tips, linear-
lanceolate, more or less erect and little contorted when dry but sometimes helically
coiled; margins strongly bordered with hyaline cells, spinose-toothed above, at least on
some leaves stoutly denticulate-toothed at shoulders; cancellinae distinct; cells of upper
lamina obscure, 5-9 | 9-14 µm, bulging-pluripapillose dorsally and ventrally. Gemmae
infrequently produced, on ventral surface of costa at leaf tips. Sporophytes unknown.

Illustrations. Reese (1978, Figs. 44-46, as S. ulei); Reese (1993, Fig. 10).
Habitat. On shaded, moist rock and soil; to 1700 m.

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24. Syrrhopodon tortilis


World range: Mexico; Central America; Caribbean, Western and Northern South America, Brazil.

The purple rhizoids, toothed leaf shoulders, large, bulging-pluripapillose leaf cells, and heavily thickened leaf margins are distinctive. In general aspect this species resembles a coarse version of Syrrhopodon prolifer var. scaber. This species was treated by Reese (1978) under the name Syrrhopodon ulei C. Mull., now a synonym of S. tortilis. The name S. tortilis Hampe was incorrectly placed in the synonymy of S. gaudichaudii Mont. by Reese (1978).

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