

A preliminary treatment of the genus *Campylopus* (Musci: Dicranaceae) in Central America

Bruce H. Allen

Missouri Botanical Garden P.O. Box 299
St. Louis, Missouri 63166-0299, U.S.A.

Abstract. There are 26 species of *Campylopus* in Central America. They are divided into three groups on the basis of two characters: the presence or absence in the costa of a ventral layer of enlarged, hyaline cells and the presence or absence in the stem of an outer hydodermis. *Dicranum costaricensis* Bartr. is transferred to *Campylopus* as *C. valerioi* nom. nov. *Campylopus hoffmanii* and *C. standleyi* are recognized as distinct species. Six new synonyms are proposed: *C. straminifolius* = *C. densicomma*; *C. costaricensis* = *C. surinamensis*; *C. roellii* = *C. tallulensis*; *C. donnellii* = *C. zygodonticarpus*; *C. tuerckheimii* = *C. zygodonticarpus*; *C. sargii* = *C. zygodonticarpus*.

The genus *Campylopus* is a large and taxonomically complex group of world-wide distribution. Frahm (1988) considers the genus to have originated in the subantarctic region of the world; in terms of species numbers the group is most diversified in Central and South America.

There is a remarkable amount of variation found in nearly all characters of *Campylopus*, and as a result the generic limits of the genus are diffuse. There is, however, a group of species that is readily recognized as belonging to *Campylopus*. This group consists of medium to large, dioicous mosses with stiff, erect to spreading, (generally unbordered), linear leaves. They have broad, excurrent costae approximately 1/2 to 2/3 the leaf width at base. The leaves in cross-section have costae with a ventral layer of variously enlarged hyaline cells (hyalocysts) and a well-developed dorsal stereid band. The upper leaf cells are firm-walled and shortly oblong, and the alar cells are differentiated. Sporophytically the setae are sinuous when moist, the exserted capsules are curved, stomata are absent, and the peristome teeth are similar to those of *Dicranum*. The calyptrae are cucullate and in many species the base of the calyptra is ciliate but the opposing character state, calyptra entire at base, is also common.

Although in the typical sense *Campylopus* is easy to recognize, the generic edges of the genus

are occupied by groups of species whose characters exhibit shades of variation in reticulate combinations. As presently understood, the only features common to all species of the genus are: 1. dioicous sexual condition, 2. broad, single, excurrent costae, 3. estomate capsules and 4. setae sinuose when moist.

A consideration of the genera near *Campylopus* makes it apparent that the above character states are generalized. The character state that has been given the greatest weight in defining the genus is the sinuous seta. The questionable value of this character state in defining *Campylopus* has been discussed by Frahm (1983). Simply stated, its presence in a number of other closely related genera, and its presence in the genus *Dicranoweisia* points to the multiple evolution of the character state in the family. Furthermore, the presence of generic pairs whose species are gametophytically nearly identical yet differ in the condition of the their setae (*Atractylocarpus-Dicranodontium*; *Dicranella-Campylopodium*; *Paraleucobryum-Campylopus p.p.*; *Pilopogon-Campylopus p.p.*) provides additional evidence that the sinuose setae has evolved several times in the group.

There have been a number of attempts at subdividing *Campylopus* (see Frahm 1982b). Usually the genus has been divided along lines corresponding to variations in the arrangement of

chlorocysts, hyalocysts, and stereid cells of the costa. But, a number of *Campylopus* species exhibit costae that are intermediate in form between two or more costal types and it has been shown (Florschütz & Florschütz-de Waard 1974) that transitional forms between subgenera can be found in serial sections of a single leaf. As a result more recent classifications of *Campylopus* do not utilize the form of the costa as seen in cross-section. Certainly, the development of dorsal stereid cells in the costa of *Campylopus* is variable to the degree that this character can not be used in subdividing the genus. On the other hand, the presence or absence of a ventral layer of thin-walled hyaline cells in the costa has not been reported to be a variable feature and in this study was found to be a diagnostic character of two groups of *Campylopus* species. Furthermore, this feature is supportive of Frahm's (1983) division of the genus into groups based on such features as capsule position, peristome shape, spore morphology, stem cross-section and costa shape as viewed from the surface.

Frahm (1983) recognized the artificial nature of *Campylopus*, but he did not give his categories generic rank on the grounds that it was not possible to vegetatively recognize them. In this study three groups of *Campylopus* could be recognized on the basis of two gametophytic characters: 1. a ventral layer of thin-walled, hyaline cells present/absent in the costa; 2. stem with/without a hyalodermis. There are 26 Central American species of *Campylopus* and for the most part they fall cleanly into the above three groups of *Campylopus*. There is one subgroup of *Campylopus*, however, that is difficult to place. This subgroup (consisting of *C. tallulensis*, *C. fragilis*, and *C. heterostachys*) has stem epidermal cells that are somewhat enlarged and variably thin-walled. The stem epidermal cells in this group may appear as a typical hyalodermis, more commonly they are only moderately enlarged and while the outer walls of the epidermal cells are thin-walled the lateral walls are usually firm-walled. The subgroup can be recognized by its basal leaf cells that are thin-walled and lax. In two members of the subgroup (*C. tallulensis* and *C. heterostachys*) the basal cells extend up the margins of the leaf in a V-shaped pattern. Since the subgroup has a costa that is gradually narrowed

into the lamina, ventral hyalocysts in the costa and erect capsules, it appears to belong to Group B of *Campylopus* (see key).

Campylopus Brid., Musc. Rec. Suppl. 4: 71. 1819.

Plants small to robust, densely tufted. Stems sparsely branched often densely tomentose, leaf rhizoids frequently arising from cells on the lower dorsal surface of the costa; stems in cross-section with a well-developed central stand of small, thin-walled, hyaline cells, inner cortex of large, hyaline to yellowish, thin- or firm-walled cells, outer cortex of smaller, thick-walled, dark-reddish cells, epidermis of enlarged hyaline cells present or absent. Leaves erect, flexuous, or spreading, ovate-lanceolate, to ovate-subulate, margins incurved, variably toothed, nearly always denticulate at the extreme apex; costa very broad below, occupying most of the leaf above, percurrent to excurrent, often ribbed or mamillate at back, at times with multi-cellular lamellae; basal cells elongate, thin-walled or incrassate, alar cells almost always present and usually well-developed, upper cells quadrate, oval, rhombic, oblong, rhomboidal or elongate, usually in oblique rows, incrassate, marginal cells at base sometimes forming a hyaline border; cells smooth, porose or entire. Dioicous. Setae strongly cygneous when moist; capsules exserted, ovoid to ellipsoid, struma present or absent, usually striate when dry, erect or curved; stomata absent; annulus present; peristome teeth haplolepidous, the 16 peristome teeth divided 1/2 to nearly their full lengths into two filaments, generally striate on the outer surface, papillose on the inner surface; opercula rostrate; calyptrae cucullate, frequently fringed at base by long, single-celled hairs. Spores 12-16 µm, yellow to brown, variously papillose.

Key to the *Campylopus* groups

1. Costae in cross-section without a ventral layer of hyaline, thin-walled cells Group A

1. Costae in cross-section with a ventral layer of hyaline, thin-walled cells 2.

2. Stems in cross-section with outermost layer of cells larger and thinner-walled than cells just below; costa gradually narrowed into the lamina Group B

2. Stems in cross-section with outermost 2-3 layers of cells small and thick-walled; costa abruptly contracted to the lamina Group C

The species of Group A are gametophytically distinct from the other members of *Campylopus* but similar to *Pilopogon*, *Dicranodontium*, *Atractylocarpus* and *Chorisodontium* in having ventral stereid cells in the costa rather than enlarged ventral hyalocysts. Only the presence of a cyneous seta separates some members of this group from the above genera. There are five representatives of group A in Central America: *C. arctocarpus*; *C. richardii*; *C. savannarum*; *C. valerioi*; *C. weberbaueri*.

Key to the Central American species of *Campylopus* Group A

1. Plants with tumid brood branches 2.
1. Plants without brood branches 3.

2. Basal leaf cells smooth and quadrate 3. *C. savannarum*

2. Basal leaf cells near costa porose and elongate 1. *C. arctocarpus*

3. Leaves with hyaline hair points 4.
3. Leaves without hyaline hair points 6.

4. Leaf cells smooth 3. *C. savannarum*

4. Leaf cells strongly porose 5.

5. All leaves with long hair points; plants without comal tufts 2. *C. richardii*

5. Only the uppermost leaves with short hyaline tips; plants with comal tufts 4. *C. valerioi*

6. Basal leaf cells smooth 3. *C. savannarum*

6. Basal leaf cells porose 7.

7. Upper leaf cells quadrate 5. *C. weberbaueri*

7. Upper leaf cells oval, oblong rhomboidal 8.

8. Leaves at base with a short, hyaline border, most leaves over 10 mm long; basal and median cells strongly porose; plants with comal tufts 4. *C. valerioi*

8. Leaves elimbate, less than 10 mm long; cells moderately porose at base only; plants without comal tufts 1. *C. arctocarpus*

1. *Campylopus arctocarpus* (Hornsch.) Mitt., J. Linn. Soc. Bot. 12: 87. 1869. *Dicranum arctocarpus* Hornsch., Fl. Bras. 1: 12. 1840. Type: Brazil, in campis montevidensibus, Sellow (not seen).

Campylopus falcatus Bartr., Contr. U.S. Natl. Herb. 26: 64. 1923. Type: Costa Rica, Heredia Province: Cerro de las Lajas, north of San Isidro, Standley & Valerio 51507 (holotype FH, isotypes NY, US; paratype Yerba Buena, Standley & Valerio 50037, NY).

Plants medium to large, tufted, dark green to yellow-brown. Stems 2-4 cm long, epidermis of small, firm-walled cells. Leaves crowded, when dry appressed to erect-spreading, at times falcate-secund, lamina distinct to apex, leaves linear-lanceolate, 3-7 mm long, apex acuminate, margins incurved above, serrate at apex. Costa percurrent to excurrent, dorsal surface mamillate to ribbed, ventral hyalocysts absent, ventral stereids weakly developed; dorsal stereids well developed. Upper laminal cells oval to rhomboidal, 8-25 µm long,

walls thickened, basal cells rectangular, walls incrassate and pitted, alar cells forming distinct groups, red-brown, walls thin. At times with short brood-branches at apex of stems. Setae 8-10 mm long, red, papillose-roughened at the apex. Capsules erect to curved, oblong, 2.0 mm long, ribbed when dry, red-brown, neck scabrose. Opercula 1.5 mm long. Calyptrae cucullate, 2.5 mm long, ciliate at base. Spores 15-18 μ m, smooth to lightly papillose, yellow.

Illustrations. Bartram (1949, Fig. 22, A-C); Florschütz (1964, Fig. 20); Crum & Anderson (1981, Fig. 94, A-F); Frahm (1978, Pl. 1).

Distribution in Central American. Guatemala (Alta Verapaz, Jalapa, San Marcos), Honduras (Morazan), Nicaragua (Jinotega), Costa Rica (Alajuela, Heredia, San Jose), Panama (Bocas Del Toro, Chiriqui, Cocle, Darien, Panama, Veraguas).

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

Selected specimens examined.

GUATEMALA. Alta Verapaz: E of Tactic, Standley 92300 (F); Jalapa: Volcan Jumay, Steyermark 32493a (F); San Marcos: 4 miles N of San Raphael, Croat 40979 (MO).

HONDURAS. Morazan: Cerro de Uyuca, Standley 4941 (F).

NICARAGUA. Jinotega: 13°02'N; 85°56'W, Stevens 5649 (MO).

COSTA RICA. Alajuela: N of Varablanca, Crosby 3758 (MO); Heredia: Yerba Buena, Standley & Valerio 50096 (NY, US); San Jose: 9°50'N; 84°07'W, Crosby 9842 (MO).

PANAMA. Bocas Del Toro: Cerro Colorado, 8°35'N; 81°45'W, Allen 5291 (MO); Chiriqui: Fortuna, Correa et al. 2285 (MO); Cocle: La Mesa, Tyson 2472N (NY); Darien: Cerro Mali, Mori & Gentry 4347 (MO); Panama: Cerro Jefe, Allen 4921 (MO); Veraguas: Cerro Tute-Arizona, 8°30'N; 81°10'W, McPherson 12067B (MO).

This species belongs to Group A of *Campylopus* a group characterized by the presence of ventral stereid bands in the costa rather than ventral hyalocysts. Within this group, *C. arctocarpus* is recognized by its porose basal leaf cells, its oval to oblong median leaf cells and its short, elimbate leaves.

In most collections of *C. arctocarpus* the leaves are stiffly erect and the basal leaf cells are distinctly porose and incrassate. A few collections of *C. arctocarpus* have plants with longer more or less secund leaves, distinctly excurrent costae and weakly porose basal leaf cells. The extreme in this expression was described by Bartram (1928) as *C. falcatus* and treated by Frahm (1979b) as a subspecies of *C. arctocarpus*. This expression is distinguished from *C. savannarum* by the presence of elongate rather than quadrate cells above the alar region.

Campylopus arctocarpus is close to the West Indian species *C. cubensis*, which has been reported from Central America as *C. harrisii*. *Campylopus cubensis* is usually separated from *C. arctocarpus* by the presence of longer upper leaf cells, more serrate leaf margins and more sharply lanceolate leaves. The examination of West Indian material of *C. cubensis* and Central American material of *C. arctocarpus* indicates that these features are variable in both species. Plants named as *C. cubensis* from Central America fall within the range of variability of *C. arctocarpus*.

2. *Campylopus richardii* Brid., Mant. Musc. 73. 1819. *Thysanomitrium richardii* (Brid.) Schwaegr., Sp. Musc. Frond. Suppl. 2: 61. 1818. 1823. *Dicranum richardii* (Brid.) C. Müll., Syn. 1: 413. 1848. *Pilopogon richardii* (Brid.) Broth., Nat. Pflanzenfam. 1(3): 336. 1901. Type: Guadelupe, Parker (not seen).

Plants medium to robust, yellowish green at tips, dark brown to black below. Stems 3-6 cm long, epidermal cells small, thick-walled, red. Leaves on fertile stems crowded above in comal tufts, appressed below, oblong-lanceolate, 3-8 mm long, apex acute, hyaline hair-pointed, margins concave below, tubulose above, entire. Costae excurrent, dorsal surface mamillate, in cross-section with small guide cells, dorsal stereid cells well-developed, ventral stereid cells weakly developed usually consisting of only a single layer. Upper laminal cells obliquely rhomboidal, basal cells linear-rectangular, all incrassate-pitted, alar cells forming distinct groups of red-yellow bulging cells. Setae 4-8 mm long, red-black, rough above. Capsules erect symmetric,

cylindrical-ellipsoid, 1.5-2.0 mm long, scabrose at base, red-black. Opercula rostrate, 1 mm long. Calyptrae cucullate, 2 mm long, ciliate at base.

Illustrations. Bartram (1949 Figs. D-H); Frahm (1978 Pl. 21); Frahm (1979 p. 177).

Distribution in Central American. El Salvador (Santa Ana); Costa Rica (Cartago, Heredia, San Jose); Panama (Bocas Del Toro, Chiriqui, Panama).

Habitat. On gravel and soil of road banks, and exposed rocks; 900-3447 m.

Selected specimens examined.

EL SALVADOR. Santa Ana: Monte Cristo, Watson 46 (MO).

COSTA RICA. Cartago: La Ascencion, 9°36'N; 83°46'W, Crosby & Crosby 6134 (MO); Heredia: 18 km N of San Jose, 10°06'N; 84°03'W, Crosby 10933b (MO); San Jose: 10 km SSE of San Jose, 9°50'N; 84°07'W, Crosby 9828 (MO).

PANAMA. Bocas Del Toro: Cerro Colorado, 8°35'N; 81°45'W, Allen 5286 (MO); Chiriqui: Volcan Baru, Ortega & La Bastille 988 (MO); Panama: Cerro Jeffe, Allen 5314 (MO).

Campylopus richardii is recognized by a combination of three characters: 1. hyaline hair-tipped leaves; 2. leaf cells short, incrassate and porose throughout; 3. costae with ventral stereid cells. It is likely to be confused only with *C. pilifer*, *C. paramoensis*, *C. valerioi* or the hair-tipped expression of *C. savannarum*. Both *C. paramoensis* and *C. pilifer* have ventral hyalocysts in their costae. In addition, *C. pilifer* has non-porose basal cells and dorsal lamellae on its costae, while in *C. paramoensis* the upper leaf cells are elongated and the stem has an outer layer of enlarged, hyaline cells. From *C. valerioi* it is distinguished by its non-comal tuft habit and its leaves that have longer, more consistently hyaline hair tips. The non-porose leaf cells and the quadrate basal cells of *C. savannarum* distinguish it from *C. richardii*.

Bartram (1949) reported what he considered to be atypical collections of *C. richardii* from Guatemala. All collections I have examined from Guatemala named *C. richardii* are instead *C. arctocarpus*. Bartram's (1949) illustration of the species does represent *C. richardii*.

3. *Campylopus savannarum* (C. Müll.) Mitt., J. Linn. Soc., Bot. 85. 1869. *Dicranum savannarum* C. Müll., Syn. Frond. 2: 596. 1851. Type: Surinam, in savarenosis planitiei prope Mariepaston ad flum. Saramaccam superiorem, Kegel (not seen).

Campylopus bartlettii Bartr., J. Wash. Acad. Sci. 22: 477. 1932. *Campylopus savannarum* subsp. *bartlettii* (Bartr.) Florsch., Fl. Suriname 6(1): 79. 1964. Type: Belize, Duck Run, Bartlett 12973 (F, MO, NY).

Plants medium, tufted, yellow-green. Stems densely tomentose, up to 6 cm long, branching irregularly, epidermis of small, firm-walled cells. Leaves evenly spaced, crowded erect-spreading when wet, erect-appressed to more or less flexuose 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. Costae long to short excurrent, excurrent part serrate and at times hyaline, frequently spurred, dorsal surface strongly mamillate, guide cells well developed, ventral and dorsal stereids present. Upper laminal 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, walls thin. Frequently with numerous asexual brood branches 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); Florschütz (1964, Fig. 23); Frahm (1979, p. 177).

Distribution in Central America. Belize (El Cayo); Guatemala (Baja Verapaz, Chiquimula, Quezaltenango, San Marcos, Totonicapan); Honduras (Morazan); Nicaragua (Esteli, Jinotega, Nueva Segovia); Costa Rica (Alajuela, Puntarenas, San Jose); Panama (Bocas Del Toro, Chiriqui, Panama).

Habitat. On branches in crown of shrubs and at base of trees, on rocks, and on soil of road banks; 1000-1500 m.

Selected specimens examined.

BELIZE. El Cayo: Pine Ridge, Duck Run, Bartlett 12973 (F, MO, NY).

GUATEMALA. Baja Verapaz: near Patal, Sharp s.n. (US); Chiquimula: Volcan Ipala, near Amatillo, Steyermark 30599 (F); Quezaltenango: Volcan Santa Maria between Santa Maria de Jesus and Calahuache, Steyermark 33672 (F); San Marcos: Volcan Tajumulco, along Rio Chapol, Steyermark 37135 (F); Totonicapan: road between San Francisco El Alto & Momostenango, Standley 84103 (F).

HONDURAS. Morazan: La Montanita, Standley 12360 (F).

NICARAGUA. Esteli: road from Hwy. 1 to San Nicolas, ca 9.5 km from Hwy. 1, Stevens 10367 (MO); Jinotega: region of La Montanita and Las Mesitas, west of Jinotega, Standley 10353 (F); Nueva Segovia: ca 5.2 km N of San Fernando, 13°2-3'N; 86°19-20'W, Stevens 3327 (MO).

COSTA RICA. Alajuela: San Pedro de San Ramon, Brenes 109 (F); Puntarenas: road E of S. Vito toward Sabalito, Crosby 2620 (MO); San Jose: Monteverde, James s.n. (US).

PANAMA. Bocas Del Toro: Cerro Colorado, ca 12 mi above Camp Chami, 8°35'N; 81°45'W, Allen, 5167 (MO); Chiriqui: Chami Camp vicinity of Cerro Colorado mine, Allen 4999 (MO); Panama: Cerro Campana, 8°40'N; 79°55'W, Crosby 4454 (F, MO, NY).

Within Group A, *C. savannarum* is marked by its broad leaves and the presence of numerous quadrate to shortly rectangular (frequently transversely elongate) cells just above the alar region. In addition, its usually stiffly erect-appressed leaves and frequently spurred, strongly mamilliose costa are distinctive. Although *C. savannarum* may be confused with *C. arctocarpus*, the presence in *C. arctocarpus* of elongate, porose leaf cells above the alar region and costae that are not spurred or mamilliose at back will separate the two.

The absence of ventral hyalocysts in the costa of *C. savannarum* appears to be a variable feature of the species. In some collections (eg. Breedlove, 2577) that are otherwise identical to *C. savannarum* small, poorly developed ventral hyalocysts can be found. These collections would key to *C. flexuosus*, but that species differs in its lack of quadrate basal cells, narrower leaves and unspurred costae.

Collections of *C. savannarum* can be extremely variable in upper leaf cell shape and size, in alar cell development and in the presence or absence

of a long, hyaline excurrent costa (up to 1 mm long). Robust collections with pronounced excurrent, hyaline costa and long upper leaf cells have been recognized at the species level (*C. bartlettii*) or as a subspecies of *C. savannarum* (Florschütz, 1964). As noted by Bartram (1949) and Frahm & Gradstein (1987) the development of hyaline leaf tips is so variable that formal recognition of this expression is not warranted.

Plants of *C. savannarum*, are frequently found with short tumid brood branches.

4. *Campylopus valerioi* Allen *nom. nov.*

Dicranum costaricense Bartr., J. Wash. Acad. Sci. 19: 13. 1929. Type: Costa Rica, La Palma, 1,500 m, Valerio 148 (FH, US). Non *Campylopus costaricensis* Bartr., Contr. U.S. Nat. Herb. 26: 62. 1928.

Plants large, caespitose, pale green to yellow above, fulvous brown below. Stems tomentose and comal tufted, up to 10 cm long, epidermal cells small and thick-walled. 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 weakly hyaline-tipped; basal cells long rectangular, 50-85 µm long, strongly incrassate and porose, those at the basal margins long, narrow, hyaline forming a short, distinct border, upper cells short, obliquely rhomboidal, 10-22 µm long, firm-walled, weakly porose or smooth walled, alar cells reddish brown in excavate groups; costae 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. Sporophytes unknown.

Illustrations. Bartram (1929b, Fig. 1, A-K, as *Dicranum costaricense*).

Distribution in Central America. Costa Rica (Heredia, San Jose), Panama (Bocas Del Toro).

Habitat. On tree trunks, soil and wet rocks; 1400-2040 m.

Specimens examined.

COSTA RICA. Heredia: road between San Rafael and Rio Las Vueltas, 10°05'N; 84°04'W, Stevens 13954, 13960(MO); San Jose:

La Palma, Valerio 148 (US), San Ramon, La Palma, Brenes 6216 (F), La Palma area, 10°03'N; 83°59'W, Crosby & Crosby 6260(MO).

PANAMA. Bocas Del Toro: Cerro Colorado, ca 12 mi above Camp Chami, Allen 5080(MO), Croat 69078A (MO).

Although the sporophyte of this species is not known, the width of its costae, comal tufted stems and the absence of a ventral layer of enlarged hyaline cells in the costa indicate that Bartram's *Dicranum costaricense* belongs in Group A of the genus *Campylopus*. Since the epithet *costaricense* is occupied in *Campylopus* a new name (*Campylopus valerioi*) is necessary.

Campylopus valerioi is a robust plant characterized by the presence of comal tufts, costae in cross-section with ventral stereids, upper leaves occasionally shortly hyaline-tipped, lower leaf cells strongly porose and incrassate, alar cells well-developed, upper leaf cells incrassate and obliquely rhomboidal and leaves bordered at base by a few rows of long narrow hyaline cells.

The species is similar to some forms of *Bryohumbertia filifolia* var. *longifolia* and to *C. weberbaueri*. From both species *C. valerioi* can be recognized by its short, hyaline limbidia at the base of the leaves. In addition *C. valerioi* is separated from the *Bryohumbertia filifolia* var. *longifolia* by its strongly incrassate and porose lower leaf cells, robust size, and broad leaves. It is further differentiated from *C. weberbaueri* by its short, obliquely rhomboidal upper leaf cells. In *C. weberbaueri* the upper leaf cells are quadrate. Although *C. richardii* is a smaller plant than *C. valerioi*, some confusion may arise in distinguishing the two since both have hyaline tipped leaves. *Campylopus valerioi* differs from *C. richardii* in its comal tufted habit and the fact that only the upper leaves have short hair tips. In *C. richardii*, which does not have comal tufts, all of the leaves have long hyaline hair-points.

5. *Campylopus weberbaueri* Broth., Bot. Jahrb. Syst. 56(123): 5. 1920. Type: Peru, Dept. Loreto, 1600 m, Weberbauer 4718 (not seen).

Campylopus wurdackii Robins., Bryologist 70: 319. 1967. Type: Peru, Dept. Amazonas, Prov. Chachapoyas, 2,350-2400 m, Wurdack 1524(US).

Plants large, laxly caespitose, pale green to yellow. Stems moderately red-tomentose characteristically with comal tufts, 2-6 cm long, epidermal cells small, thick-walled. Leaves 8-13 mm long, circinate above, stem leaves erect, comal leaves paten, long, narrowly lanceolate, oblong below, long subulate, serrate above; basal cells long rectangular, incrassate and porose, those at the margin narrower, forming an indistinct, non-hyaline border, upper cells quadrate, firm-walled not porose, alar cells reddish-brown, in excavate groups; costae percurrent to shortly excurrent, in cross-section at base 1/3-1/2 the leaf width, sharply serrate above at back, guide cells well developed, ventral hyalocyst absent, dorsal and ventral stereid bands well-developed. Setae 1-6 in comal tufts, 7-8 mm long, yellow. Capsules oval, inclined, plicate when dry, 1.5-2.0 mm long, strumose at base. Calyptrae cucullate, ciliate at base.

Illustrations. Robinson (1967, Figs. 8-11, as *Campylopus wurdackii*); Frahm (1978, Pl. 30).

Distribution in Central America. Panama (Bocas Del Toro).

Habitat. Corticolus on upper tree branches; 1200 m.

Specimen examined. PANAMA. Bocas Del Toro: west of Chiriqui Grande road at Continental Divide, Allen 5769(MO).

Campylopus weberbaueri is a robust plant with erect-leafed, comal tufted stems, and sharply serrate leaves with costae serrate at back. When dry the leaves are flattened at base in a manner similar to *C. jamesonii*, *C. subcuspidatus* or *C. standleyi*. The presence on the ventral surface of the costae of stereids rather than hyalocysts separates *C. weberbaueri* from these species.

From other members of *Campylopus* Group A *C. weberbaueri* is distinguished by its robust size and quadrate upper leaf cells. There are two species (*Bryohumbertia filifolia* var. *longifolia*

and *C. valerioi*) that are similar to *C. weberbaueri* in having comal tufted stems, serrate costae, and leaves serrate on the upper margins. *Campylopus weberbaueri* is separated from *Bryohumbertia filifolia* var. *longifolia* by its more robust size, and broader leaf apices and from *C. valerioi* by its elimbate leaves and its quadrate upper leaf cells.

Campylopus Group B

Members of *Campylopus* Group B are distinguished from Group C (both groups have a layer of ventral hyalocysts in the costa) by their stem hyalodermis and by their costa which in cross-section does not have the dorsal stereid band extending to the costal margins. As a consequence, the edges of the costa, as seen in cross-section are made up of several layers of enlarged, thin-walled cells. It is necessary to make cross-sections of the stem in order demonstrate a hyalodermis in this group. It is important to remember when making stem sections that the leaves should not be stripped from the stem since the hyalodermal cells adhere to the base of the costa when the leaves are removed. There are several species in Group B that have a weakly developed stem hyalodermis, for that reason the placement of a species within this group relies on both the presence of a stem hyalodermis and a distinctive costal structure. It may be useful to note that a few of the species in this group either lack stereid cells or have only pseudostereids. Finally, *C. paramoensis* is only reluctantly placed in Group B since it does not have the distinctive costal structure of the group. For this reason it is included in the keys to both Group B and Group C. There are 8 species of Group B in Central America: *C. albidovirens*; *C. aerodictyon*; *C. cavifolius*; *C. fragilis*; *C. heterostachys*; *C. nivalis*; *C. paramoensis*; *C. tallulensis*.

Key to the Central American species of *Campylopus* Group B

1. Plants with brood leaves or brood branches 2.
1. Plants without brood leaves or brood branches 4.
2. Plants with masses of sessile, brood leaves 9. *C. fragilis*
2. Plants with tumid brood branches 3.
3. 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 cells absent 6. *C. albidovirens*
3. 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 7. *C. aerodictyon*
4. Leaves with hyaline hair-points and narrow, elongated leaf cells throughout 12. *C. paramoensis*
4. Leaves without hyaline hair-points; upper leaf cells quadrate to rhomboidal 5.
5. Marginal leaf cells at base rectangular, thin-walled and more or less bulging 6.
5. Marginal leaf cells at base linear, narrow, firm-walled forming a distinct border 8.
6. Enlarged, hyaline basal leaf cells extending upwards at the margin in a v-shaped pattern; alar cells present (at times fugacious) 7.
6. Enlarged, hyaline basal leaf cells grading evenly into the quadrate median leaf cells; alar

cells absent 9. *C. fragilis*

7. Alar cells well-developed; leaves serrate above 10. *C. heterostachys*

7. Alar cells poorly-developed, frequently fugacious; leaves denticulate on at the extreme apex 13. *C. tallulensis*

8. 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 6. *C. albidovirens*

8. Leaves narrowly lanceolate, long narrowly acuminate to setaceous; costa in cross-section with rounded, non-interdigitating guide cells; dorsal stereids or pseudostereids present 9.

9. Leaves over 10 mm long 8. *C. cavifolius*

9. Leaves less than 10 mm long 10.

10. Leaves spreading secund when dry; upper leaf cells oblong-rectangular, 3-5 x 14-22 μm long 10. *C. nivalis*

10. Leaves stiffly erect when dry; upper leaf cells quadrate, 3-7 x 5-12 μm long 7. *C. areodictyon*

6. *Campylopus albidovirens* Herz., Biblioth. Bot. 87: 19. 1916. Type: Bolivia, uber Tablas, ca 3400m, Herzog 2782 (not seen).

Campylopus guatemalensis Bartr., Bryologist 49: 110. 1946. Type: Guatemala, Dept. Quetzaltenango, Standley 86159 (holotype, FH).

Plants slender to medium, compactly tufted, pale greenish- yellow with a slight greyish sheen when dry and somewhat glossy. 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 to 7/8 the leaf width at base; dorsal surface smooth or mamilllose; 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 leaf cells quadrate to oblong, incrassate, not porose; basal cells long-rectangular, laxly thin-walled, hyaline, those at the basal margin forming an indistinct 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 , smooth, yellow.

Illustrations. Herzog (1916, Pl. 1, fig. 12); Bartram (1949, Fig. 18, A-E); Frahm (1978, Pl.2).

Distribution in Central America. Guatemala (Huehuetenango, Quezaltenango, Totonicapan); El Salvador (Santa Ana); Costa Rica (Cartago, San Jose).

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

Selected specimens examined.

GUATEMALA. Huehuetenango: between Soloma & San Jose, Sharp 4976 (F); Quezaltenango: Cerro Quemado, above Los Vahos, Standley 86137 (F, FH); Totonicapan: between Huehuetenango and Sija, Standley 83101a (F, FH).

EL SALVADOR. Santa Ana: Monte Cristo, Watson 40 (MO).

COSTA RICA. Cartago: montanas alrededor del Valle de Los Lagos, Chirripo, Espinach & Morales 784 (MO, USJ); San Jose: Sierra e Talamanca, Cerro de la Muerte, Schultes 174 (FLAS), 17 km SE of El Empalme, 9°37'N; 83°48'W, Crosby 10945 (MO), summit of Pan American highway at Cerro la Muerte, 9°30'N; 83°45'W, Crosby 3903 (MO).

Although *C. albidovirens* is known in Central America only from a few localities the species has been collected in Mexico and along the Andes as far south as Chile. It is distinguished from most other *Campylopus* species by its pale greenish-yellow color (frequently greyish as seen for example in *Paraleucobryum longifolium*), the

absence in the costa of dorsal stereid cells, and the presence of enlarged, pentagonal guide cells that interdigitate at their apex with the ventral hyalocysts. The arrangement of guide cells and ventral hyalocysts in *C. albidovirens* is similar to that seen in *Paraleucobryum*. This combination of character states also occurs in *C. pittieri*, a species reported from Central America. In *C. albidovirens*, however, the alar cells are weakly developed (but frequently fugacious), the leaves are narrower and more linear, the costa is widest at base, and the setae are 5-7 mm long. In contrast *C. pittieri* lacks alar cell development, the leaves are shorter and thicker (resembling those of *Paraleucobryum enerve*), the costa is narrowed at base, and the setae are up to 14 mm long. All Central American material of *C. pittieri* I examined is *C. albidovirens*. *Campylopus pittieri* does, however, occur in Mexico and Colombia.

Campylopus albidovirens is most likely to be confused with *C. nivalis* (= *C. chrismarii*) which has a similar color and dorsal pseudostereids in its costae. Although in *C. albidovirens* the leaves are shorter and broader and the calyptrae are fringed while in *C. nivalis* the leaves are long and narrowly lanceolate, the calyptrae entire, to properly separate these two species cross-sections of the costa must be examined. In *C. albidovirens* dorsal stereid cells are clearly lacking and the guide cells, which are pentagonal shaped, interdigitate with the ventral hyalocysts. In *C. nivalis* the development of pseudostereids is such that it is difficult (and sometimes impossible) to decide if stereids are present or absent. Furthermore, the guide cells of *C. nivalis* are rounded, thick-walled and do not interdigitate with the ventral hyalocysts.

Superficially, *C. albidovirens* looks like a larger version of *Campylopodia flagellacea*, but in *C. flagellacea* the costa in cross-section has both ventral and dorsal hyalocysts, a median band of stereids and 2-4 layers of stereids present on the ventral surface of the costa near the center.

7. *Campylopus areodictyon* (C. Müll.) Mitt., J. Linn. Soc., Bot. 12: 85. 1869. *Dicranum areodictyon* C. Müll., Syn. Musc. Frond. 1: 394. 1848. Type: Colombia, Prov. Merida e Sierra Nevada alt. 9000 ft, Funck & Schlim in coll Linden 1082

(isotype NY).

Campylopus subconcolor (Hampe) Mitt., J. Linn. Soc., Bot. 12: 86. 1869. *Dicranum subconcolor* Hampe, Linnaea 32: 138. 1863. Type: Colombia, Bogota La Penna, Lindig 2013b. (FH).

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, epidermis in cross-section consisting of enlarged thin-walled cells. 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, up to 5/8 the leaf width at base, in cross-section the ventral hyalocysts well developed, 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 μ m, incrassate, not porose; basal cells long rectangular, hyaline, thin-walled, marginal cells long, narrow, firm-walled, forming a limbidium 6-12 cells wide; alar cells weakly developed, red-brown to hyaline, thin-walled. Occasionally with short, tumid brood branches in upper parts of the stem. Sporophyte not seen.

Illustrations. Frahm (1978, Pl. 2 & Pl. 24 as *C. subconcolor*); Frahm (1980b, Figs. 17, 18, as *C. subconcolor*).

Distribution in Central American. Costa Rica (Cartago, San Jose); Panama (Chiriqui).

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

Specimens examined.

COSTA RICA. Cartago: 97 km S of Cartago along Interamerican highway, Bowers 414A (US); San Jose: Cerro de la Muerte, Koch 5088 (US); San Jose-Cartago: Cordillera de Talamanca, Cerros Cuerici, 9°35'N; 83°38'30"W, Davidse et al. 24861, 24818 (MO).

PANAMA. Chiriqui: summit of Cerro Pavon, Hammel & D'Arcy 6438 (MO), summit of El Barú, Croat 34941 (MO).

Campylopus areodictyon, a South American

species more generally known as *C. subconcolor*, is easily confused with *C. nivalis* (= *C. chrismarii*). Both species have weakly developed dorsal stereids in the costa (usually present as pseudostereids) and a well developed basal limbidium. Typically, *C. nivalis* has a pale, whitish-yellow color, and secund leaves while in *C. areodictyon* the leaves are dark, greenish-yellow and erect to appressed. Technically the species are distinguish by the differences in the size and shape of their upper leaf cells as given in the key.

From *C. albidovirens*, a species with appressed leaves that lacks dorsal stereids in its costa, *Campylopus areodictyon* is distinguished by its narrowly lanceolate leaves, shiny dark greenish-yellow color, entire calyptrae and thick-walled, rounded guide cells. In *C. albidovirens* the leaves are broadly lanceolate, the plants are pale yellow-green, the calyptrae are fringed and the enlarged, thin-walled guide cells are sharply angled and interdigitate with the ventral hyalocysts.

8. *Campylopus cavifolius* Mitt., J. Linn. Soc., Bot. 12: 87. 1869. Types: Andes Quitenses, in montibus Chimborazo Cordovasto, Titaicun, Spruce 50 (not seen); Jameson (not seen).

Plants large, compactly tufted, greenish-yellow, frequently dark reddish-yellow, more or less glossy. Stems moderately tomentose, up to 8 cm long, epidermis in cross-section having a hyalodermis consisting 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 made up 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, large rectangular near the costa 40-65 μm , becoming narrow and elongate toward the margins forming a distinct border up to 10 cells wide; alar cells reddish, weakly developed, frequently

fugacious or remaining on stem when leaves are stripped. Sporophytes not seen.

Illustrations. Frahm (1978, Pl. 5).

Distribution in Central American. Panama (Chiriqui).

Habitat?

Specimen. PANAMA. Chiriqui: Bois de Boquete near David, Helion (S, specimen not seen).

Campylopus cavifolius is a large plant with stiffly erect, setaceous leaves that are distinctly bordered in the lower half by up to 10 rows of narrowly, elongated cells. In cross-section the dorsal stereid band of its costa is present only in the center, at the margins the costa is made up of 2-3 layers of enlarged, thin-walled cells. Although this type of costal structure is found in a number of other species, it is nowhere as well-developed as in *C. cavifolius*. The only Central American species likely to be confused with *C. cavifolius* is *C. areodictyon*, which also has stiffly erect leaves, a similar costal cross-section, and leaves with a basal border of elongated cells. However, in *C. cavifolius* the leaves are larger (10-12 mm vs. 5-7 mm) and the upper leaf cells are longer (elongate, 20-50 μm vs. quadrate, 10-12 μm).

I have seen no material of *C. cavifolius* from Central America, Frahm (1982) cited the above specimen from Panama. The above description of the species is based on an examination of South American material.

9. *Campylopus fragilis* (Brid.) B.S.G., Bryol. Eur. 1:164. 1847. *Dicranum fragile* Brid., J. Bot. 1800(2): 296. 1801. Type: Germany, Erlangen, Hoffmann s.n. (not seen.)

Plants small, tufted, green to yellow-green. Stems usually densely tomentose, 0.6-3.5 cm long, epidermal cells moderately enlarged and variably thin- to firm-walled. Leaves 3-5 mm long, erect-paten, more or less flexuous above when dry, lanceolate, oblong below, subulate above, serrulate toward the apex; basal cells rectangular, hyaline, thin-walled, bulging, in

dried material frequently remaining full of air upon wetting, marginal basal cells narrower but not forming a distinct border, cells just above the hyaline basal cells firm-walled, quadrate, upper cells rhomboidal, alar cells absent; costae 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 costae therefore made up of 2-3 layers of enlarged hyaline cells. Minute, slender brood leaves 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).

Distribution in Central America. Guatemala (Alta Verapaz, Huehuetenango, Quetzaltenango, Quiche, San Marcos, Totonicapan); Costa Rica (San Jose).

Habitat. On humus, rotting logs and soil; 2500-3130 m.

Selected specimens examined.

GUATEMALA. Alta Verapaz: 2-3 mi. S of Purulha, Croat 41757 (MO); Huehuetenango: pass between Barillas & San Mateo, Sharp 4939a (FH); Quezaltenango: above Quezaltenango, Sharp 1995 (FH); Quiche: Above Nibaj, Sharp 2484 (MO, NY, US); San Marcos: 3.3 mi above San Rafael, Croat 40918 (MO); Totonicapan: along road between San Francisco El Alto and Momostenango, Standley 84107 (F).

COSTARICA. San Jose: 10 km NW of La Ascension, 9°37'N; 83°48'W, Crosby & Crosby 6128 (MO).

Campylopus fragilis belongs to a subgroup of *Campylopus* Group B that has stem hyalocysts only moderately enlarged and frequently only thin-walled to the outside. It is characterized by enlarged hyaline cells throughout the leaf base, an absence of alar cells, and the presence of brood leaves at the apex of the stems. The brood leaves in *C. fragilis* are identical to those found in *Brothera leana*. Indeed, Guatemalan specimens

named *B. leana* by Bartram represent small collections of *C. fragilis* that consist almost entirely of brood leaves. The two species are distinguished by the distribution of stereid cells in their costae and the shape of their upper leaf cells. In *C. fragilis* dorsal stereid cells are present below the guide cells and the upper leaf cells are quadrate. In *B. leana* the costa has a ventral and dorsal layer of hyalocysts, a median layer of stereid cells and long rectangular upper leaf cells. The only other Central American species of *Campylopus* with brood leaves is *C. trichophorus*. From that species *C. fragilis* is distinguished by its sessile brood leaves (stalked in *C. trichophorus*) smaller size, lack of alar cell development, and enlarged thin-walled basal cells.

Some difficulty may be encountered in separating *C. fragilis* from *C. tallulensis*, another species of this subgroup of Group B with weakly developed stem hyalocysts and enlarged, thin-walled basal cells. In *C. tallulensis* the hyaline basal cells continue up the margins of the leaves forming a V-shaped pattern, in *C. fragilis* all of the hyaline basal cells end at about the same level in the leaf. In addition, in *C. tallulensis* alar cells, although variably developed and frequently fugacious, are differentiated. The alar cells of *C. tallulensis*, when fugacious, are represented by rounded gaps in the alar region of the leaves.

10. *Campylopus heterostachys* (Hampe) Jaeg., Ber. Thatigk. St. Gallischen Naturwiss. Ges. 1870-71: 421. 1872. *Dicranum heterostachys* Hampe, Flora 48: 581. 1865. Type: Peru. Prov. Carabaya, prope Sandia ad rivulis Tuche, 4000 ft, Hasskarl s.n. (not seen.)

Plants medium, greenish-yellow. Growing in dense mats, stems moderately to densely tomentose, up to 8 cm long but frequently less than 3 cm long, simple to sparingly branched, epidermal cells thin-walled, somewhat larger than the outer cortical cells, hyaline. 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. Lower basal cells rectangular, 35-40 µm long, at the margins a few

rows extending upwards forming a v-shape pattern; upper basal, median and upper cells quadrate 5-12 μm ; alar cells well-developed, red-brown extending to the costa and frequently in excavate groups. Costae shortly excurrent, concolorous, 1/2 to 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 the stereid band not as wide as the costa, the margins of the costa consisting of 2-3 layers of enlarged cells. Setae 6-7 mm long, red. Capsule curved, furrowed when dry, 1.5-2.0 mm long. Opercula conic-subulate, 1.0-1.2 mm long. Spores not seen. Calyptrae cucullate, smooth at base.

Illustrations. Frahm (1978, Pl. 12).

Distribution in Central America. Guatemala (Huehuetenango, Quezaltenango, San Marcos); Honduras (Morazan); Costa Rica (Alajuela, Cartago, Heredia, San Jose); Panama (Chiriqui).

Habitat. On bark of trees, rotting logs, and terrestrial; 1050- 2600 m.

Selected specimens examined.

GUATEMALA. Huehuetenango: between Todos Santos and San Martin, Sharp 4808 (MO, US); Quezaltenango: above Mujulia between San Martin Chile Verde and Colomba, Standley 85675 (F, NY); San Marcos: Barranco Eminencia, above San Rafael Pie de la Cuesta, Standley 86229 (F, FH).

HONDURAS. Morazan: La Motanita, Standley 12357 (F).

COSTA RICA. Alajuela: vicinity of Fraijanes, Standley & Torres 47460 (US); Cartago: vic of Orosi, Standley 39703 (US); Heredia: Cerros de Zurqui, NE of San Isidro, Standley & Valerio 50273 (FH); San Jose: Valle de Copey ca 30 km S of Cartago, Griffin & Morales B95 (F).

PANAMA. Chiriqui: Cerro Colorado, 8°35'N; 8°45'W, Allen 5220 (MO).

Most collections of *C. heterostachys* from Central America have been called *C. hellerianus* and treated by Bartram (1949) as a synonymy of *C. flexuosa*. The species has a very broad costa which, as is characteristic of plants in Group B, has the stereid band in the lower 1/3 of the leaf not as wide as the costa. As seen from above the costa grades into the lamina and in cross-sections the margins of the costae consist of 2-3 layers of

enlarged thin-walled cells. This feature is variably expressed in *C. heterostachys*; at times it is present only at the very base of the leaf. Usually the leaves of *C. heterostachys* are flattened at the base when dry which makes the leaves appear very broad. This feature is also found in *C. jamesonii*, *C. subcuspidatus*, and *C. standleyi*.

Unlike most members of Group B, *C. heterostachys* does not have a distinct border of narrow, elongated, hyaline cells at the base of the leaf. Instead, the basal marginal cells are rectangular, hyaline and variably firm- to lax-walled. Characteristically, these enlarged basal cells extend upwards along the margins forming a v-shaped pattern. This type of leaf border is also seen in *C. talluensis*, which also has the same type of costal cross-section and stem epidermal cells. In *C. heterostachys*, however, the upper leaf margins are variously serrate and the alar cells are well-developed while in *C. talluensis* the leaves are denticulate only at the extreme apex and the alar cells are poorly developed, frequently fugacious.

All Central American collections of *C. concolor* have, in this study, been referred to *C. heterostachys*. The two species appear to be very close and in fact a few of the collections originally named *C. concolor* do not fit comfortably in *C. heterostachys*. In the past the two have been separated by differences in their basal leaf cells: *C. heterostachys* - thin-walled; *C. concolor* - thick-walled. This distinction appears to be unreliable since it is possible to find a series of leaves from a single plant that will show both types of cells. In this study *C. concolor* is separated from *C. heterostachys* by its larger leaves (over 10 mm), lower basal leaf cells that do not extending upwards at the margins in a V-shaped pattern, and by its dorsal stereid band in the costa which in cross-section is as wide as the costa.

Special care is needed in order to distinguish *C. heterostachys* from some collections of *C. andersonii*. Both species have quadrate upper leaf cells and lower basal cells that are similarly enlarged. In *C. andersonii*, however, the leaves are not flattened at 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.

11. *Campylopus nivalis* (Brid.) Brid., Bryol. Univ. 1: 477. 1826. *Weisia nivalis* Brid., Spec. Musc. 1: 123. 1806. *Dicranum nivale* (Brid.) Spreng., Syst. Veg. 4: 167. 1827. *Thysanomitrium nivale* (Brid.) Arnott, Mem. Soc. Linn. Paris 5:263. 1827. Type: Reunion, "In Insulae Bourbonis monte Pithon des neiges", Bory de Saint Vincent. (not seen.)

Dicranum chrismarii C. Müll., Bot. Zeitung 13: 761. 1855. *Campylopus chrismarii* (C. Müll.) Mitt., J. Linn. Soc., Bot. 12: 88. 1869. Type: Mexico, Province Mechoacan, Chrismar (isotype NY).

Dicranum friabile Hampe in C. Müll., Bot. Zeitung 17: 220. 1859. *Campylopus friabilis* (Hampe) Jaeg., Ber. Tatigk. St. Gallischen Naturwiss. Ges. 1870-71: 432. 1872. Type: Costa Rica, Los Nubes, Wendlaub (isotype NY).

Campylopus poasensis Ren & Card., Bull. Soc. Roy. Bot. Belgique 31: 148. 1893. Type: Costa Rica, sommet du Volcan Poas, Pittier 5511 (isotype NY).

Plants slender to medium in size, tufted, pale yellow-green, usually glaucous. Stems 10 cm long, stem 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, bordered at base by several rows of narrow, elongated, hyaline cells. Costae 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 laminal cells oblong-rectangular to hexagonal 14-22 mm long, walls thickened not porose, basal cells laxly rectangular, those near the costae enlarged, hyaline, thin-walled and bulging, those at the margins forming a distinct hyaline border; alar cells weakly differentiated, frequently fugacious, red-brown, thin wall. 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 (1985, Figs. 63-64).

Distribution in Central America. Guatemala (Chimaltenango, Huehuetenango, Quezaltenango, Quiche, San Marcos, Tontonicapan); Costa Rica (Alajuela, San Jose); Panama (Bocas del Toro, Chiriqui).

Habitat. On soil, fallen logs, tree trunks and branches in open pastures or shaded, wet forests; 1800-4400 m.

Selected specimens examined.

GUATEMALA. Chimaltenango: Volcan de Acatenango, Standley 61847 (F); Huehuetenango: above San Mateo, Sharp 4945 (F); Quezaltenango: Volcan Santa Maria, Steyermark 34182 (F, NY); Quiche: between Quiche and San Pedro Jocopilas, Standley 62461 (FH); San Marcos: Volcan Tacana, Steyermark 36104 (F); Tontonicapan: region of Desconsuelo, Standley 62688 (F).

COSTA RICA. Alajuela: Volcan Poas, Griffin & Araya 47 (F, MO, NY); San Jose: Cerro de la Muerte, Crosby 3905 (MO).

PANAMA. Bocas Del Toro: Cordillera de Talamanca, Cerros Fabrega, 9°07'N; 82°52'40"W, Davidse et al. 25298A (MO); Chiriqui: Volcan Baru, Beliz & Correa 911 (MO).

Campylopus nivalis has generally been known in Central America as *C. chrismarii*. The two taxa were synonymized by Frahm (1985). The species has a glaucous color, narrow, erect-spreading leaves, a well defined basal leaf border, lax basal cells, broad costae (up to 5/8 the leaf width at base) and in the dorsal region of the costae a short band of poorly developed stereids that are usually termed pseudostereids. *Campylopus nivalis* belongs to a group of species marked by a costal cross-section in which the stereid cells are restricted to the central part while the lateral margins consist of several layers of enlarged, thin-walled cells, a well-developed hyaline border on the base of the leaves, and a stem that has an outer layer of enlarged, hyaline cells.

There are two other Central American species (*C. aerodictyon* and *C. albidovirens*) that have

pseudostereids or no stereid development in the costa that may be confused with *C. nivalis*. From *C. aerodictyon*, *C. nivalis* is distinguished by its glaucous color, erect-spreading leaves, and oblong-rectangular upper leaf cells that are from 14-22 μm long. By contrast, in *C. areodictyon* the plants are shiny yellowish-green, the leaves are stiffly erect, and the rounded to quadrate upper leaf cells are from 5-12 μm long.

Both *C. albidovirens* and *C. nivalis* are similar in color, habit and the presence of enlarged, hyaline, thin-walled basal leaf cells. The presence of pseudostereids in *C. nivalis* and the absence of any stereid development in *C. albidovirens* separates the two, however, without the benefit of experience pseudostereids can be difficult to recognize. One should keep in mind that in *C. albidovirens* the absence of stereid cells is obvious and the pentagonal, sharply angled guide cells have the point of the pentagon interdigitating with the ventral hyalocysts. In *C. nivalis* the guide cells are rounded, and the stereid cells are developed to the degree that it becomes difficult to decide if stereids are present. Also, the calyptrae are entire in *C. nivalis* but fringed in *C. albidovirens*.

12. *Campylopus paramoensis* F. Bowers, Bryologist 77: 152. 1974. Nomen novum for *Campylopus atratus* Bartr., Contr. U.S. Natl. Herb. 26: 61. 1928. non *Campylopus atratus* Broth., Trans. Linn. Soc. London, Bot. ser. 2, 6: 89. 1901. Type: Costa Rica, San Jose, Cerro de las Vueltas, Standley & Valerio 43686 (holotype FH, isotypes NY, US).

Plants compact in slender to medium tufts, reddish-yellow above, blackish below. Stems reddish, radiculose, up to 3 cm long; epidermis of enlarged thin-walled cells. Leaves evenly spaced, when wet erect-spreading, when dry stiffly erect-appressed, strongly concave to tubulose, lanceolate-subulate, 3-7 mm long, margins entire below denticulate at apex, marginal cells more or less elongated but not forming a distinct border. Costae 2/3 the leaf width at base, excurrent as a hyaline hair-point, smooth at back, ventral hyalocysts large, well developed; guide cells and dorsal stereids well developed. Upper laminal cells linear-flexuose to linear, 35 μm x 3-5 μm ,

walls incrassate with rounded end walls, basal cells short rectangular to rhomboidal, walls incrassate, alar cells forming distinct groups of reddish to hyaline, thin-walled cells. Sporophytes unknown.

Illustrations. Bartram (1928, Fig. 4, A-F).

Distribution in Central America. Costa Rica (San Jose).

Habitat. On wet bank; 2700-3000 m.

Specimen examined. COSTA RICA. San Jose: Cerro de las Vueltas, Standley & Valerio 43686 (FH, NY, US).

Campylopus paramoensis is the only member of Group B that has hyaline hair-pointed leaves. Other noteworthy features are its incrassate leaf cells that are linear-flexuose above and porose at base and its sharply differentiated alar cells. *Campylopus paramoensis* resembles *C. richardii* in its color, its strongly incrassate, elongated leaf cells and its hyaline hair-tipped leaves. In *C. paramoensis*, however, the costa has ventral hyalocysts instead of ventral stereid cells, the stem has a layer of enlarged hyaline cells rather than small, thick-walled cells and the upper leaf cells are more linear-flexuose. *C. paramoensis* is the only species in Group B that lacks the distinctive costal structure characteristic of the group. It is placed in Group B solely on the strength of its stem hyalodermis.

13. *Campylopus tallulensis* Sull. & Lesq. ex Sull., Icones Muscorum 27. 1864. Type: Georgia, Tallulah Falls, Lesquereux (isotypes MO, NY, US).

Campylopus roellii Ren. & Card., Bull. Soc. Roy. Bot. Belgique 38: 9. 1900. Type: Costa Rica, Juan Vinas, 3400 m, Sarg (isotype US). 1865. *syn. nov.*

Plants medium, sordid-green to yellow-green. Growing in dense tufts, stems moderately to densely tomentose, up to 3 cm long, simple to sparingly branched, inner cortical cells firm-walled, yellow-red, outer cortical cells smaller, thicker walled, dark red, epidermal cells enlarged but firm-walled. 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, entire below, more or less toothed at the extreme apex. 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; upper basal cells quadrate to rectangular, chlorophyllose, firm-walled; upper cells shortly rectangular to quadrate, firm-walled; alar cells poorly developed, frequently fugacious. Costae percurrent to shortly excurrent, 1/3 to 1/2 the leaf base, smooth to lightly ribbed at back, in cross-section with ventral hylocysts, 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. 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. Calyptrae 2.0-2.5 mm long, cucullate, fringed at base. Opercula rostrate, 1.0 mm long.

Illustrations. Sullivan (1864, pl. 17); Grout (1937, Pl. 50A); Frahm (1978 Pl. 27); Crum & Anderson (1981).

Distribution in Central America. Belize (Cayo); Guatemala (Guatemala); Honduras (Comayagua); Costa Rica (Cartago); Panama (Chiriqui).

Habitat. On soil, rocks and logs in forest; 900-3300m.

Selected specimens examined.

BELIZE. Cayo: Mountain Pine Ridge, 17°00'N; 88°47'W, Davidse & Brant 33056A (MO).

GUATEMALA. Guatemala: Volcan de Pacaya, Standley 80620 (FH).

HONDURAS. Comayagua: Honduras road no. 1, 9.2 mi N of Siguatepeque, Crosby 2809 (MO).

COSTA RICA. Cartago: Juan Vinas, Roll s.n. (US).

PANAMA: Chiriqui: Volcan Baru, 8°45'N; 82°30'W, McPherson 9477i (MO).

Campylopus tallulensis is a medium sized, yellow-green plant. Its erect to appressed leaves

are shortly acuminate, essentially entire (they may be somewhat serrulate at the extreme apex) and the leaf lamina is present nearly to the apex. Characteristically, the lower basal leaf cells are enlarged, hyaline, and continue up the margins in a distinctive V-pattern. The upper basal and median leaf cells are quadrate, firm-walled and chlorophyllose and contrast strongly with the lower basal cells. In the illustrations accompanying Sullivan's original description of this species the alar cells are figured as well-developed and fairly firm-walled, but type material and collections from Central America have alar cells that are poorly developed and frequently fugacious. In the lower 1/3 of the leaf *C. tallulensis* has the dorsal stereid band not as wide as the costa. As a result the margins of the costa in cross-section are made up of 2-3 layers of enlarged cells. This feature is also found in *C. heterostachys* and *C. fragilis*, the two species most likely to be confused with *C. tallulensis*.

Campylopus tallulensis is separated from *C. heterostachys* by its essentially entire leaves and poorly developed to fugacious alar cells. In *C. heterostachys* the leaves are spinous-serrate above and the alar cells are well developed. *Campylopus tallulensis* is best separated from *C. fragilis*, which also has entire leaves and poorly developed alar cells, by the V-pattern of hyaline cells on the basal margins. In *C. fragilis*, the enlarged basal cells grade evenly into the quadrate median cells and the plants usually have numerous brood leaves. Asexual brood bodies are not found in *C. tallulensis*.

Bartram (1949), placed *C. roellii* under the synonymy of *C. flexuosus*. *Campylopus roellii* is treated here as a synonym of *C. tallulensis*.

The collection of *C. tallulensis* from Honduras (Crosby 2809) is a first report of sporophytes for this species.

Key to the Central American species *Campylopus*, Group C.

1. Plants with brood leaves or brood branches 2.
1. Plants without brood leaves or brood branches 2.

- ches 3.
2. Plants with tumid brood branches 17. *C. flexuosus*
2. Plants with masses of stalked brood leaves 15. *C. asperifolius*
3. Leaves with hyaline hair points 4.
3. Leaves without hyaline hair points 7.
4. Costa with 2-3 celled dorsal lamellae in the upper one-third 22. *C. pilifer*
4. Costa smooth to mamillate on dorsal surface 5.
5. Upper leaf cells narrowly elongate *C. paramoensis* (see Group B)
5. Upper leaf cells rhomboidal 6.
6. Hyaline hair points present on all vegetative and perichaetial leaves 23. *C. oerstedianus*
6. Hyaline hair points present only on some comal leaves 25. *C. surinamensis*
7. Basal leaf cells porose 8.
7. Basal leaf cells smooth 13.
8. Costa 2/3 or more the leaf width at base; leaves at base appearing flattened when dry 9.
8. Costa at base 1/3 to 1/2 the leaf width; leaves concave at base when dry 10.
9. All basal leaf cells strongly porose; leaves with a narrow hyaline border at base; upper leaf cells oblong 24. *C. subcuspidatus*
9. Inner basal leaf cells porose, outer basal leaf cells smooth-walled; leaves elimbate; upper leaf cells oval 23. *C. standleyi*
10. Costae 1/3 the leaf width; leaves spreading from the base when dry; costa in cross-section with ventral hyalocysts less than 1.5 x the size of the guide cells; stem apices pectinate 18. *C. hoffmanii*
10. Costa 1/2 the leaf width; leaves erect at base when dry; costa in cross-section with ventral hyalocysts up to 2 x the size of the guide cells; stem apices flexuous 11.
11. Median leaf cells quadrate 14. *C. andersonii*
11. Median leaf cells oblong to elongate 12.
12. Leaves subulate; leaf apices flexuous but not spirally twisted when dry 16. *C. densicoma*
12. Leaves acuminate; leaf apices spirally twisted when dry 15. *C. asperifolius*
13. Costa in cross-section with ventral hyalocysts smaller than or as large as the guide cells 14.
13. Costa in cross-section with ventral hyalocysts much larger than the guide cells 17.
14. Alar cells well-developed, frequently auriculate 17. *C. flexuosus*
14. Alar cells poorly developed, not auriculate 15.
15. Leaves subulate, lamina quickly narrowed from an ovate base, juxta-costal basal cells enlarged, shortly rectangular, contrasting sharply with the narrower, longer, thicker-walled outer basal cells; capsules erect when dry 26. *C. zygodonticarpus*
15. Leaves lanceolate, lamina gradually narrowed, extending nearly to the apex, juxta-costal basal cells not sharply contrasting with the outer basal cells; capsules curved when dry 16.

16. Leaf apex of upper comal leaves strongly dentate and at times subhyaline; costa dorsally mamilllose above 25. *C. surinamensis*
16. Leaf apex smooth to weakly serrulate, concolorous; costa dorsally smooth above 20. *C. lamprodictyon*
17. Median leaf cells oblong to elongate 18.
17. Median leaf cells quadrate 19.
18. Leaves subulate; leaf apices flexuous, not spirally twisted when dry 16. *C. densicoma*
18. Leaves acuminate; leaf apices spirally twisted when dry 15. *C. asperifolius*
19. Leaves more than 10 mm long AND the costa over 1 mm wide at base 19. *C. jamesonii*
19. Leaves 10 mm or less long AND the costa less than 1 mm wide 14. *C. andersonii*

14. *Campylopus andersonii* (C. Müll.) Jaeg., Ber. Tatigk. St. Gallischen Naturwiss. Ges. 1870-71: 436. 1872. *Dicranum andersonii* C. Müll., Bot. Zeit. 14: 169. 1856. Type: Ecuador, Galapagos Islands, Charles Island, Andersson (H, not seen).

Plants medium sized, tufted, greenish-yellow, moderately shiny. Stems variably white or reddish tomentose, up to 6 cm long, epidermis in cross-section consisting of small, thick-walled, dark red cells. Leaves linear, variable in size 6-10 mm long; flexuous to distinctly secund when dry, slenderly setaceous above, narrowly concave below, serrate to serrulate above. Costa excurrent, 1/2 to 2/3 the leaf width at base; dorsal surface smooth or lightly mamilllose; in cross-section with enlarged ventral hyalocysts, stereid band well developed and extending to the edge of the costa. Upper and median leaf cells quadrate, 12-

25 µm 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 µm, lightly roughened, yellow.

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. subinacorrallis*).

Distribution in Central America. Guatemala (Quezaltenango, San Marcos), Costa Rica (Cartago, Heredia, Puntarenas, San Jose), Panama (Bocas Del Toro).

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

Selected specimens examined

GUATEMALA. Quezaltenango: Volcan Santa Maria, Steyermark 34325 (F, FH); San Marcos: road between San Marcos and San Rafael Pie de la Cuesta, Standley 86300 (F, FH).

COSTA RICA. Cartago: El Muneco, on the Rio Navarro, Standley & Torres (FH, NY, US); Heredia: Laguna Barba, 10°05'N; 83°55'W, Crosby 10928 (MO); Puntarenas: Monteverde, James s.n. (US); San Jose: ca 7 km N of Santa Maria de Dota, Standley 43016 (US).

PANAMA. Bocas Del Toro: Cerro Colorado, 8°35'N; 81°45'W, Allen 5051A (MO).

Most of the Central American collections of *C. andersonii* fit the expression of the species previously known as *C. longisubulatus*. In that expression the leaves are long and slenderly setaceous, nearly over 10 mm long. This expression is recognized by its large leaves, costae with ventral hyalocysts and a well developed dorsal stereid band that extends to the costal margins, and quadrate median leaf cells. *Campylopus jamesonii*, the only other species with this combination of characters, can be distinguished from *C. andersonii* by its wider costae (over 1 mm

vs. less than 1 mm). There are expressions of the *C. andersonii* with leaves much less than 10 mm long that can be difficult to distinguish from *C. heterostachys*. *Campylopus andersonii* has elimbate leaves that are rounded below when dry, a costal stereid band which extends outward to the margins of the costa and stem epidermal cells that are small and thick-walled. In *C. heterostachys* the leaves are flattened below when dry, the costal stereid band does not reach the margins of the costa, its basal leaf cells extend upward along the margins a short distance in a v-shaped pattern, and its stem epidermal cells are somewhat inflated and thin- to firm-walled. In Central American material these features are variably expressed and it may be that what has been called *C. andersonii* and *C. heterostachys* in Central America is actually the same thing. There are also expressions of *C. andersonii* with more or less porose basal cells near the costa that may be confused with *C. densicoma*. The two species differ fundamentally in the shape of their median leaf cells: *C. andersonii* - quadrate; *C. densicoma* - oblong to elongate.

15. *Campylopus asperifolius* Mitt., J. Linn. Soc., Bot. 12: 79. 1869. Types: Ecuador, Andes Quitenses, Spruce 54, (lectotype PC, Frahm 1981, not seen); Chile, Andes Chilenses, Tatanara, Lechler 2627 (syntype, not seen).

Campylopus trichophorus Hampe ex Herz., Biblioth. Bot. 87: 20. 1916. Type: Bolivia, Herzog 2858, 4447, 5055 (not seen).

Plants medium to large, tufted, pale green to yellow. Stems moderately red-tomentose, up to 4 cm long, epidermal cells small, thick-walled. Leaves 4-6 mm long, erect-paten when dry, frequently with twisted apices; erect-spreading when wet, lanceolate, ovate at base, concave below, serrate at the apex, at time serrulate in the upper 1/4, basal cells long rectangular, 60-100 μm long, cells at the margins narrower, and thinner but not hyaline, median and upper cells obliquely rhomboidal, 12-20 μm long, all cells firm-walled, not porose (rarely with a few juxtacostal cells at the extreme base weakly porose; alar cells red-brown, well-developed, extending to the costae but not bulging in excavate groups; costae shortly

excurrent, concolorous, 1/3 to 1/2 the leaf width at base, smooth or lightly mamillate on dorsal surface, in cross-section guide cells well developed, ventral hyalocyst much larger than guide cells, dorsal stereids well developed. Masses of brood-leaves, each arising from a long stalk, commonly present at the stem apex. Sporophyte not seen.

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

Distribution in Central America. Belize (Belize); Costa Rica (Alajuela, Cartago, San Jose); Panama (Bocas Del Toro, Chiriqui).

Habitat. On the upper branches of trees, occasionally on trunks and terrestrial; 80-3130 m.

Specimens examined.

BELIZE. Belize: 4 km W of Hattieville, 17°26'N; 88°25'W, Davidse & Brant 32958 (MO).

COSTA RICA. Alajuela: Volcan Poas, Valerio 282 (US); Cartago: 97 km S of Cartago along Interamerican Highway, Bowers 308-H (US), Tapanti Hydroelectric Reserve along Rio Grande de Orosi, Croat 36095 (MO); San Jose: 10 km NW of summit at La Ascension, Crosby & Crosby 6108 (MO), 17 km SE of Empalme 9°37'N; 83°48'W, Crosby 9762 (MO).

PANAMA. Bocas Del Toro: Cerro Colorado, 8°35'N; 81°45'W, Allen 5048, 5284 (MO), Croat 33229B (MO), Fortuna Dam-Chiriqui Granderoad, 8°45'N; 82°15'W, McPherson 6790A (MO), Allen 5723, 5740 (MO), 5 mi below Continental Divide on Chiriqui Grande side, Allen 5567 (MO); Chiriqui: vicinity of Boquete, Croat 66498 (MO).

This species, reported from Central America as *C. trichophorus*, is recognized by its clusters of brood leaves that occur on long stalks in the upper leaf axils. The only other Central American species of *Campylopus* with brood leaves (as opposed to brood branches) is *C. fragilis*. *Campylopus asperifolius* is distinguished from that species by its stalked brood leaves, firm-walled basal cells, and well developed alar cells. In *C. fragilis* the brood leaves are sessile, the basal cells are lax, thin-walled and bulging throughout and the alar cells are absent.

Plants of *C. asperifolius* without brood leaves may be confused with *C. densicoma* or *C. hoffmanii*. *Campylopus densicoma* has subulate,

non-twisted leaf apices and flexuous leaves when dry. In *C. asperifolius*, the apices are acuminate and often twisted, and the leaves are more stiffly erect when dry. In both species the leaves may have a few porose cells near the costa at the extreme leaf base.

Although both *C. hoffmanii* and *C. asperifolius* have distinctive pencillate tipped stems, in *C. hoffmanii* the leaves are long subulate and spread from the base when dry. *Campylopus asperifolius* has acuminate leaves and erect leaf bases.

16. *Campylopus densicoma* (C. Müll.) Par., Ind. Bryol. Suppl. 91. 1900. *Dicranum densicoma* C. Müll., Nuov. Giorn. Bot. Ital. 4:33. 1897. Type: Bolivia, provincia Cochabamba prope Choquecamata, alto-montose, 10,000-12,000 ft, June 1889, Germain (Müller no. 1120, NY).

Campylopus straminifolius Bartr., Contr. U.S. Natl. Herb. 26: 63. 1928. Type: Costa Rica, Cartago Prov., El Muneco, Rio Navarro, Standley & Torres 51212 (NY, US). *syn. nov.*

Plants medium sized, green to yellowish green. Stems lightly to moderately tomentose, 3-4 cm long, epidermal cells small and thick-walled. Leaves 8-11 mm long, erect-patent to erect-flexuous below, flexuous above, lance-subulate, concave throughout, serrate above in the upper 1/4, basal cells long rectangular 60-100 µm long, firm-walled, cells near the costa porose, those at the margins narrower, not forming a hyaline border, median cells rhomboidal 15-35 µm firm-walled, not porose, upper cells short-rectangular to quadrate, 10-17 µm long, firm-walled, alar cells red-brown in large bulging groups, extending to the costae; costae excurrent, concolorous, 1/2 the leaf width at base, smooth to lightly mamillate at back; in cross-section with ventral hyalocysts larger than guide cells, dorsal stereids well developed. Sporophytes three to six at apex of stem in comal tufts; setae 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. Spores oval, 12-15 µm. Calyptrae entire at base.

Illustrations. Bartram (1928, Fig. 6, A-I as *C.*

straminifolius); Frahm (1978, Pl. 8; Pl. 11 as *C. gertrudis*);

Distribution in Central America. Costa Rica (Alajuela, Cartago, Heredia, Puntarenas, San Jose); Panama (Bocas Del Toro).

Habitat. On bamboo, tree stumps and soil; 1050-3150 m.

Specimens examined.

COSTA RICA. Alajuela: SE slope of Volcan Poas, Gomez 20014 (MO); Cartago: El Muneco on the Rio Navarro, Standley & Torres, 51212 (NY, US); Heredia: Las Vueltas area, ca 18 km N of San Jose, Crosby & Crosby 6455 (MO); Puntarenas: Cordillera de Talamanca, Cerro Echandi, 9°01'30"N; 82°49'W, Davidse et al. 23947 (MO); San Jose: Cerro de las Vueltas, Standley 43538a (FH, US).

PANAMA. Bocas Del Toro: Cordillera de Talamanca, 4 km NW of Cerro Fabrega, 9°09'N; 82°54'W, Davidse et al. 25410 (MO).

Campylopus densicoma is a slender, flexuous plant with concolorous leaves, usually porose basal cells and costae with ventral hyalocysts and a well developed stereid band. The porose basal cells in this species are not always easy to demonstrate (see e.g. the type of *C. straminifolius*), and the species can be confused with *C. andersonii* which also has a similar habit. Separation of these species relies on the presence in *C. andersonii* of quadrate median leaf cells and enlarged, bulging juxtacostal cells. In contrast, *C. densicoma* has elongate to oblong median cells and inner basal cells that are firm-walled.

Bartram (1949) 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.

17. *Campylopus flexuosus* (Hedw.) Brid., Mant. Musc. 4: 71. 1819. *Dicranum flexuosum* Hedw., Spec. Musc. 145. 1801. Type: Germany, Densa cohorte in sylvis, copiose circa Gissam, Dillenius (not seen.).

Campylopus mexicanus Thér., Smithsonian Misc. Collect. 78: 7. 1926. Type: Mexico. Mi-

choacan State, vic. Morelia, Campanario, Broadward 7576 (MO, US).

Campylopus hondurensis Bartr., Field Mus. Nat. Hist., Bot. Ser. 4: 351. 1929. Type: Honduras, In pine forest, El Achote near Siguatepeque, Dept. Comayagua, February 18, 1928 Standley 56157a (US), 56149a (F).

Plants small, tufted, yellow-green. Stems variably tomentose, 1.5-2.0 cm long, commonly with numerous brood branches at the apex, inner cortical cells thick-walled, yellow, outer cortical cells small, thick-walled, red, epidermal cells small firm-walled. Leaves 3-5 mm long, erect-patent, erect, or somewhat falcate-secund when wet, appressed to flexuose when dry, concave, lanceolate, apex acute to short acuminate, margins entire or a few teeth present at the extreme apex, not border by elongated cells. Costae percurrent to shortly excurrent, in cross-section 1/2 to 2/3 the leaf width, at times with low mamillae, guide cells well developed, dorsal stereids present, ventral hyalocysts present but mostly smaller than (at times equal to) the size of the guide cells. Leaf cells firm-walled, not porose; upper laminal cells irregularly oval to short rectangular, 10-20 μm long; median cells irregularly rectangular, basal cells rectangular, usually firm-walled; alar cells differentiated, forming reddish-brown to hyaline auricles. Setae 4-7 mm long, red-yellow. Capsule 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 to 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 , smooth, yellow-green.

Illustrations. Bartram (1929, Pl. 17, Figs. A-J); Bartram (1949, Fig. 19, A-D); Crum & Anderson (1981, Fig. 99, H-K).

Distribution in Central America. Guatemala (Alta Verapaz, Guatemala, Jalapa, Quezaltenango, Quiche, Totonicapan); El Salvador (Santa Ana); Honduras (Comayagua, Morazan); Costa Rica (Cartago, Heredia); Panama (Chiriqui).

Habitat. On decomposing logs and tree trunks;

1000-3333 m.

Selected specimens examined.

GUATEMALA. Alta Verapaz: 2-3 mi. S of Purulha, Croat 41764A (MO); Guatemala: Volcan de Pacaya above Las Calderas, Standley 58424 (F); Jalapa: Volcan Jumay, Steyermark 32489 (F); Quezaltenango: Chiquival, Sharp 2073 (MO); Quiche: above Nebaj, Sharp 2525 (US); Totonicapan: between Huehuetenango and Sija, Standley 62664 (F).

EL SALVADOR. Santa Ana: Monte Cristo, Watson 35 (MO).

HONDURAS. Comayagua: El Achote, near Siguatepeque, Standley 56157A (US); Morazan: Campamento de Las Flores, Cerro de Uyuca, Standley 13726 (F).

COSTA RICA. Cartago: Dos Amigos, SE of El Empalme, Crosby & Crosby 6356 (MO); Heredia: Volcan Barba, Hatheway & Hatheway 1715 (US).

PANAMA. Chiriqui: Fortuna, Salazar et al. 545 (MO), 9 km WNW of Boquete, Davidse & D'Arcy 10329E (MO).

Bartram (1949), taking a broad view of this species, considered *C. flexuosus* to be "exceedingly variable." The species is treated here in a much more restricted sense. In fact, Bartram's concept of *C. flexuosus* is here considered to encompass five distinct species: *C. surinamensis* (as *C. gracilicaulis*); *C. heterostachys* (as *C. hellerianus*); *C. tallulensis* (as *C. roellii*); *C. zygodonticarpus* (as *C. sargii*, *C. donneli*, *C. subleucogaster*); and *C. densicoma* (as *C. straminifolius*).

Campylopus flexuosus frequently has tumid brood branches at the apex of stem and this is one of easiest ways of recognizing the species. Confusion with other *Campylopus* species with brood branches is unlikely since *C. flexuosus* is the only one of that group that has ventral hyalocysts in the costa that are smaller than or as large as the guide cells. Care should, however, be taken when examining collections of *C. savannarum* with brood branches. Although, *C. savannarum* lacks ventral hyalocysts, its ventral stereid band is not well developed and the cells are somewhat larger than typical stereid cells. *Campylopus savannarum* can also be recognized by its numerous thick-walled, quadrate basal leaf cells.

When brood branches are absent some difficulty may be encountered in separating *C. flexuosus* from *C. lamprodictyon*, *zygodonticarpus*, and *C. surinamensis*. All four species have

small-sized ventral hyalocysts in cross-section, but in *Campylopus flexuosus* the alar cells are distinctly differentiated while in the other three species the alar cells are poorly developed or absent.

18. *Campylopus hoffmannii* (C. Müll.) Ren & Card., Bull. Soc. Roy. Bot. Belgique 31(1): 147. 1893. *Dicranum hoffmannii* C. Müll., Linnaea 38: 592. 1874. Type: Costa Rica, in paludibus montis vulcanici de Barba, Hoffmann s.n. (not seen).

Campylopus nematophyllus Ren. & Card., Bull. Soc. Roy. Bot. Belgique 31(1): 147. 1893 *nom. invalid.* Type: Costa Rica, Forêts du Barba, versant pacifique, 2700-2500 m, 1890 Tonduz [Pittier 5509] (FH, NY).

Plants large, slender, yellow-green. Stems moderately tomentose, up to 17 cm long, epidermal cells small thick-walled. Leaves 8-14 mm long, widely spaced, erect-spreading below, pinnate at apex, when wet spreading from an ovate base, long, slenderly setaceous above, concave throughout, serrate above; basal cells incrassate and porose, long rhomboidal to linear, those at the margins narrower and shorter but not forming a distinct border, upper cells shortly rectangular, 12-25 µm, firm-walled; alar cells well developed, red-brown in large, excavate groups extending to the costae, firm-walled. Costae 1/3 or less the leaf width at base, shortly excurrent, concolorous, smooth to lightly ribbed on back; in cross-section with well developed guide cells, ventral hyalocysts present, frequently only a little larger than the guide cells, dorsal stereid band well-developed. 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.

Illustrations. None.

Distribution in Central America. Guatemala (Guatemala); Costa Rica (Heredia, Limon, Puntarenas, San Jose); Panama (Bocas Del Toro).

Habitat. On trees, wet banks, and in Sphagnum bogs; 1640-3000 m.

Selected specimens examined.

GUATEMALA. Guatemala: Amatitlan, Volcan Pacaya, Kellerman s.n. (FH, US).

COSTA RICA. Heredia: Cerros de Zurqui, NE of San Isidro, Standley & Valerio 50511 (FH, NY, US); Limon: Cerros Tararia, 9°09'N; 82°58'W, Davidse et al. 28835 (MO); Puntarenas: Monte Verde, Fielder 101 (MO); San Jose: Laguna de la Chonta, NE of Santa Maria de Dota, Standley 42331 (FH, NY, US).

PANAMA. Bocas Del Toro: trail from Boquete to Cerro Pate Macho, 8°49'N; 82°24'W, McPherson & Merello 8314E (MO).

Campylopus hoffmannii is a distinctive species that can be recognized in the field by its large size, its long, slender, distantly spaced leaves that spread from the base at right angles to the stem, and its pinnate stem apices. The species is likely to be confused only with *C. subcuspidatus* or *C. standleyi* which also are large plants that have strongly porose leaf cells. From those species *C. hoffmannii* is distinguished by its small ventral hyalocysts in the costae, relatively narrow costae and its narrower leaves that are concave at the base when dry.

Frahm (1978) placed *C. hoffmannii* into the synonymy of *C. cuspidatus*. However, 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, have concolorous, setaceous apices and rhomboidal upper leaf cells. In Central America the distinctive characters of *C. hoffmannii* do not intergrade with those *C. cuspidatus*.

19. *Campylopus jamesonii* (Hook.) Jaeg., Ber. Tatigk. St. Gallischen Naturwiss. Ges. 1870-71: 422. 1872. *Dicranum jamesonii* Hook., Icon. Pl. 2: 179. 1837. Type: Colombia, Surucucho, Jameson (not seen.)

Campylopus standleyi var. *lutescens* Bartr., Contr. U.S. Natl. Herb. 26: 60. 1928. Type: Costa Rica, Prov. San Jose, Santa Maria de Dota, Standley & Valerio 43372 (FH, NY, US).

Plants robust, greenish-yellow. Growing in dense mats, stems moderately to densely tomentose, up to 12 cm long, simple to sparingly

branched, epidermal cells small, thick-walled. Leaves spreading below, erect-spreading above, concave when wet, flattened when dry, lanceolate-setaceous, up to 20 mm long, serrate in upper 1/4 to 1/2. 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; median cells firm-walled, quadrate, apical cells quadrate; alar cells well-developed in large groups extending to the costae and frequently excavate. Costae excurrent, concolorous, up to 4/5 the leaf width at base, smooth to lightly mamilliose, in cross-section guide cells well-developed, large ventral hyalocysts present, dorsal stereids well-developed. (Sporophyte description from Hooker) Setae 15 mm long. Capsules curved, furrowed when dry strumose at base. Operculum conic-subulate.

Illustrations. Hooker (1837, Pl. 179, Figs. 1-9); Frahm (1978, Pl. 14); Frahm (1979, page 176); Frahm (1985, Fig. 50).

Distribution in Central America. Costa Rica (San Jose).

Habitat. Terrestrial, on shady road banks; 1500-3220 m.

Specimens examined.

COSTA RICA. San Jose: vicinity of Santa Maria de Dota, Standley & Valerio 43372 (FH, US), Cerro de la Muerte, 3 mi N of El Empalme, Croat 32887b (MO), 4.1 km NW of Cerro Asuncion, 9°36'N; 83°46'W, Stevens 14350 (MO), 13 km SE of El Empalme, 9°40'N; 83°51'W, Crosby & Crosby 7221 (MO), Cerro Daser, 5 km S of Asseri, 9°50'N; 84°07'W, Crosby 9820 (MO).

In Central America *C. jamesonii* is likely to be confused only with *C. standleyi*. Both are large plants with leaves flattened at the base when dry, but in *C. jamesonii* the leaves are longer (up to 20 mm), the leaf cells are smooth-walled throughout, the basal leaf cells above the alar cells are lax and enlarged, the marginal cells at the base short rectangular to quadrate, and the leaves are serrate in the upper 1/4 to 1/2. In *C. standleyi* the leaves

are less than 15 mm long, the juxtacostal cells at base are porose, the basal cells above the alar cells are rectangular, firm-walled and not particularly enlarged, the marginal leaves at the base are narrow and elongate and the leaves are serrulate only at the extreme apex. Unfortunately, there are a number of collections that are intermediate in some of the characteristics given above. For a discussion of these problem collections see *C. standleyi*.

There are two other large Central American species (*C. subcuspidatus* and *C. heterostachys*) that when dry have broad, flattened costae. *Campylopus subcuspidatus* differs from *C. jamesonii* in its porose leaf cells, short hyaline border of elongated, narrow cells, and its leaves that are serrulate only at the extreme apex. *Campylopus heterostachys* is similar to *C. jamesonii* in its smooth-walled cells and its leaves that are serrate in the upper 1/2 to 1/3. It differs in its smaller size (leaves less than 13 mm) in having firm-walled, quadrate basal cells above the alar region, a stem hyalodermis and a costa that is not sharply distinguished from the lamina.

20. *Campylopus lamprodictyon* (Hampe) Mitt., J. Linn. Soc., Bot. 12: 82. 1869. *Dicranum lamprodictyon* Ann. Sci. Nat. Bot. ser. 5, 5: 339. 1866. Type: Colombia, Bogota, Cipacon, 2600 m, Lindig (not seen.)

Plants medium sized, forming dense greenish-yellow tufts. Stems tomentose at base, up to 3.0 cm long, unbranched or with single branches occurring beneath comal tufts, epidermal cells small, thick-walled, dark red. Leaves flexuous at base, becoming abruptly appressed to the stem, then crowded and spreading in apical comal tufts; growth continued by means of a lateral branch from beneath the comal tuft, 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 those of the comal tuft long-subulate; all leaf margins concave below, tubulose above, not bordered by elongated cells, weakly serrate at apex, usually entire below. Upper cells rhombic, median cells rhomboidal, both 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. 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. Sporophytes unknown in Central America.

Illustrations. Frahm (1978, Pl. 15).

Distribution in Central America. Costa Rica (Cartago).

Habitat. Rotting tree fern; 2680 m.

Specimen examined. COSTA RICA. Cartago: Dos Amigos area, SE of El Empalme, 9°37'N; 83°50'W Crosby & Crosby 6351 (MO).

This species is very similar to *C. surinamensis* differing only in the weakly serrulate, concolorous leaf apices, and dorsally smooth costae. In *C. surinamensis*, the leaf apices are strongly dentate, the comal leaves may be hyaline tipped and the costae are mamillate at the back. As with *C. surinamensis* and other species with comal tufts the leaves from a single plant are remarkably variable depending upon the position of the leaf on the plant. Basal leaves, appressed stem leaves, and comal tuft leaves differ not only in size and shape, but also in the form of their cells. Alar cells may be absent on some leaves and present in others.

Frahm (1987) placed a number of species with comal leaves under the name *C. pauper* (including this species as *C. pauper* var. *lamprodictyon*). These taxa are separated from *C. surinamensis* by the absence of a basal rosette of leaves and the presence in the perichaetial leaves of concolorous apices. The presence, in the costa, of ventral hyalocysts that are equal in size or smaller than the guide cells is an important feature that links *C. lamprodictyon* and *C. surinamensis*. In Central America the only features that will consistently separate the two species are the smooth costae and

the weakly serrate leaf margins of *C. lamprodictyon*.

21. *Campylopus oerstedianus* (C. Müll.) Mitt., J. Linn. Soc., Bot. 12: 81. 1869. *Dicranum oerstedianus* C. Müll., Bot. Zeit. 9: 259. 1851. Type: Costa Rica, Volcan de Irazu, 11,000 ft, Oersted (isotype NY).

Plants small, densely tufted, yellowish-green above, brownish below. Stems densely red-tomentose below, up to 1.0 cm high, unbranched, epidermal cells small, dark-red, thick-walled. Leaves typically erect-appressed, subtubulose above, occasionally leaves on stem becoming tightly appressed then forming a comal tuft of more or less flexuous-spreading leaves; leaves 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 and sharply serrulate; 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 lax-walled; alar cells weakly differentiated, reddish or hyaline in slightly auriculate groups. Costa percurrent to short-excurrent (perichaetial leaves excurrent as an awn), in cross-section with ventral hyalocyst equal to or smaller than the guide cells, dorsal stereid band well-developed. Sporophyte unknown.

Illustrations. Frahm (1975, Fig. 14); Frahm (1980, Figs. 4-9); Crum & Anderson (1981, Fig. 99L-O).

Distribution in Central American. Costa Rica (Cartago).

Habitat. On tree; 3750 m.

Specimen examined. COSTA RICA. Cartago: Volcan Irazu, Oersted s.n. (NY).

Campylopus oerstedianus has consistently in the past been compared to *C. pilifer* on account of its short hyaline leaf tips. The two species are

best distinguished by the presence of dorsal lamellae on the costae of *C. pilifer*. In *C. oerstedianus* costal lamellae are absent.

This species appears to be nearest to *C. surinamensis* as indicated by their similar leaf shape, areolation, and costal cross-section in which the ventral hyalocyst are equal to or smaller in size than the guide cells. The difference in their vegetative leaf tips (hyaline in *C. oerstedianus*, concolorous in *C. surinamensis*) is minimized by the presence of hyaline leaf tips in the perichaetial leaves of *C. surinamensis*. *Campylopus oerstedianus* is near to a group of *Campylopus* (which includes *C. surinamensis*, *C. lamprodictyon*, and *C. pauper*), that is characterized by small ventral hyalocysts and the tendency to have a comal-tuft morphology. Interestingly, *C. pilifer* also has small ventral hyalocysts and a comal tuft morphology; but its relationship to this subgroup of *Campylopus* is uncertain. Although the comal-tuft morphology is weakly developed to absent in *C. oerstedianus*, its presence is erratic in the other members of the group. Future study may show this group to be members of a single variable species. At present *C. oerstedianus* is maintained as distinct from *C. surinamensis* on the basis of its smaller plant size, weakly developed comal-tuft morphology and hyaline tipped vegetative leaves.

22. *Campylopus pilifer* Brid., Musc. Recent. Suppl. 4: 72. 1819. Types: Italy, in *Insula Ischia* 1806 (lectotype B, Gradstein & Sipman 1978, not seen); France, in *saxis sylvae prope Fontainebleau* 1807 (not seen.)

Plants small to medium, tufted, yellow-green to brownish- yellow. Stems variable in length, 1.0-6.5 cm long, branches few and irregularly spaced, epidermis of small, firm-walled cells. Leaves crowded, erect-spreading when wet, appressed when dry, leaves oblong-lanceolate, 3-6 mm long, subulate at apex and ending in a long, toothed, hyaline hair-point, up to 1.9 mm long, margins subtubulose above, entire below, denticulate at apex. Costae excurrent, dorsal surface with 2-6 celled lamellae in the upper 2/3 of the leaf; in cross section with ventral hyalocysts smaller or slightly bigger than the guide cells,

dorsal stereids well developed. Upper leaf cells oval to oblong, incrassate not pitted, smooth, 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*); Frahm 1978, Pl. 19); Frahm (1979, page 177); Crum & Anderson (1981, Fig. 96); Frahm (1985, Fig. 73).

Distribution in Central America. Belize (Cayo, Toledo); Guatemala (Alta Verapaz, Baja Verapaz, Chimaltenango, Escuintla, Guatemala, Huehuetenango, Jalapa, Jutiapa, Quezaltenango, Quiche, Sacatepequez, San Marcos, Solola, Totonicapan); El Salvador (Chalatenango, San Miguel, Santa Ana, Sonsonate); Honduras (Comayagua, El Paraiso, Morazan); Nicaragua (Jinotenga, Managua, Masaya); Costa Rica (Alajuela, Cartago, Heredia, Puntarenas, San Jose); Panama (Chiriqui, Panama).

Habitat. On soil, along roadsides and in forest, bare rock, lava, occasionally on logs and trees; 300-3500 m.

Selected specimens examined.

BELIZE. Cayo: Along Rio Or, San Augustin, Mains 4068 (F, US), Mains 4070 (F, NY); Toledo: lower slopes of Richardson Peak, Maya Mountains, 16°34'N; 88°46'W, Davidse & Brant 32180 (MO).

GUATEMALA. Alta Verapaz: between Coban and Chichen Tactic, Tuerkheim s.n. (NY); Baja Verapaz: near Jicaro, Sharp 2668 (US); Chimaltenango: Volcan Acatenango, Kellerman s.n. (US); Escuintla: Pacaya Volcano, Egger 523 (NY); Guatemala: Volcan Pacaya, between San Francisco Sales and the base of the active cone, Standley 80732 (F); Huehuetenango: Rio Pucal, ca 14 km S of Huehuetenango, Standley 82308 (F, NY); Jalapa: Cerro Alcoba, Steyermark 32602 (F, NY); Jutiapa: between Jutiapa and Plan de Urrutia, north of Jutiapa, Standley 75594 (F); Quezaltenango: along Rio Samala, near Santa Maria de Jesus,

Standley 84735 (F, NY); Quiche: above Nebaj, Sharp 2538 (US); Sacatepequez: near Antigua, Standley 58816 (F); San Marcos: road above Barranco Eminencia, Standley 68535 (F); Solola: ca 18 miles W of Quezaltenango, Hermann 26339 (F, NY); Totonicapan: between San Francisco El Alto and Momostenango, Standley 84103 (NY).

EL SALVADOR; Chalatenango: Cayagua, San Ignacio, Winkler 20 (MO); San Miguel: Volcan San Miguel, Egger 701 (NY); Santa Ana: Volcan de Santa Ana, Al norte del Volcan, do de Palo Campana, Winkler 29 (MO); Sonsonate: Volcan Izcalco, Egger 705 (NY).

HONDURAS; Comayagua: vicinity of Siguatepeque, Standley 55844 (F, US); El Paraiso: south of Guinope, Standley 14867 (F); Morazan: El Hatillo, 10 kms NE of Tegucigalpa, Pilz 1421 (MO).

NICARAGUA; Jinotega: ca 2 miles NW of Jinotega on road to San Rafael del Norte, Croat 43028 (MO); Managua: E-W ridge along Hwy 8 ca 0.4 km from Hwy 2 intersection, 11°58'N; 86°18-19'W, Stevens 4547 (MO); Masaya: N slope of Volcan Santiago, 11°59'N; 86°10'W, Stevens 5289 (MO).

COSTA RICA; Alajuela: 14 km SW of San Ramon, Crosby 3615 (MO); Cartago: Cartago, Alfaro 118 (F, US); Heredia: vicinity of Varea Blanca, Croat 35539A (MO); Puntarenas: Monte Verde, Crosby 2486 (MO); San Jose: 17 km SE of El Empalme, 9°37'N; 83°48'W, Crosby 9759 (MO).

PANAMA; Chiriqui: ridge S of Cerro Horqueta, N of Boquete, Crosby 4006 (MO); Panama: Cerro Campana, 8°40'N; 79°55'W Crosby 4355 (MO).

This moss has generally been known in Central America as *C. introflexus*, an essentially south temperate moss also found in Europe and North America (Gradstein & Sipman 1978, Frahm 1980). *Campylopus pilifer* is recognized by the presence of 2-6 celled lamellae on the back of its costae, its long, hyaline, serrate, leaf hairpoints, and the presence of enlarged, hyaline, thin-walled basal leaf cells. Dorsal lamellae are always present on the costa, however, the height of the lamellae and the number of lamellae are variable. Two expressions *C. pilifer* are present in Central America: one having plants with comal tufts at the ends of long erect stems bearing rigidly appressed leaves, the other with plants lacking comal tufts and having stiffly erect leaves with incurved apices.

Campylopus pilifer is likely to be confused only with *C. surinamensis* or *C. savanarum*. These species may at times have hyaline tipped leaves and strongly mamilliose costae that could be

mistaken for lamellae. The multi-celled lamellae and the enlarged, hyaline, thin-walled basal cells of *C. pilifer* are not found in either species.

23. *Campylopus standleyi* Bartr., Contr. U.S. Natl. Herb. 26: 59. 1928. Types: Costa Rica, Prov. San Jose, Cerro de las Vueltas, Standley & Valerio 43939 (FH, NY, US). Paratypes, Costa Rica, Prov. San Jose, Las Nubes, Standley 38639 (FH, NY, US); Finca la Cima, Standley 42696a (FH, NY, US).

Plants robust, yellowish-green. Stems moderately to densely tomentose, up to 15 cm long, epidermal cells small, in 3-4 layers. Leaves flexuous when dry, lanceolate, subulate, gradually narrowed to a long, filiform point from an ovate-oblong base, laminae extending nearly to the apex, serrulate at apex, smooth below, 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. Costae shortly excurrent, concolorous, up to 4/5 the leaf width at base, smooth to lightly mamilliose at back; in cross-section guide cells well-developed, large ventral hyalocysts present, dorsal stereids well-developed. Sporophytes single; setae 12-14 mm long, smooth. Capsules curved, furrowed when dry, more or less strumose, 2 mm long. Opercula 1.5 mm long, conic-rostrate, oblique. Calyptrae cucullate, entire at base, 2 mm long.

Illustrations. Bartram (1928, Fig. 2, A-J); Bartram (1949, Fig. 20).

Distribution in Central America. Guatemala (Huehuetenango); Costa Rica (Cartago, Puntarenas, San Jose); Panama (Bocas Del Toro, Chiriqui).

Habitat. Terrestrial, rotting wood and tree trunks; 1050-3700 m.

Selected specimens examined.

GUATEMALA. Huehuetenango: summit of Sierra de los

Cuchumatanes, Steyermark 50188a (F, FH).

COSTA RICA. Cartago: Cerro Las Vueltas, Holm & Iltis 1101 (FH, US), 9 mi. SW of El Empalme, Woodruff 14988 (US), Dos Amigos, SE of El Empalme, 9°37'N; 83°50'W, Crosby & Crosby 8592 (MO); Puntarenas: Cordillera de Talamanca, NW of Las Alturas, Davidse 24350a (MO); San Jose: Copey, Valerio 414 (FH), 97 kms S of Cartago, Griffin, Canessa & Eakin 19946 (NY, US), Cerro de la Muerte, Koch 5090 (NY, US), Croat 32885 (MO), Crosby 3912 (MO), 17 km SE of El Empalme, Crosby 10886 (MO), La Ascension, Crosby & Crosby 6114 (MO).

PANAMA. Bocas Del Toro: Cordillera de Talamanca, Cerro Fabrega, 9°07'N; 82°05'40"W, Davidse et al. 25298 (MO); Chiriqui: Cerro Colorado, 8°35'N; 81°45'W, Allen 4995, 5010 (MO), Volcan Baru, D'Arcy et al. 12560A (MO).

Campylopus standleyi is a robust species with a broad costa that occupies nearly 4/5 the leaf width at base. The costae and therefore the leaves are flattened when dry giving the plants a distinctive appearance. There are three other large Central American species of *Campylopus* with similarly flattened leaves: *C. jamesonii*, *C. subcuspidatus* and *C. heterostachys*. *Campylopus heterostachys* is a smaller plant, with distinctly bulging alar cells and several rows of quadrate cells just above the alar cells. The other three members of this group are macroscopically nearly identical and while typically they are well marked, troublesome intermediates exist.

Campylopus subcuspidatus, a Caribbean species also found in Belize, Surinam and Brazil, has strongly porose cells in the lower half of the leaf, a hyaline leaf border of narrow, elongated cells in the lower 1/4 to 1/2, elongated upper leaf cells, and leaf margins that are serrulate at the apex but entire below.

Campylopus standleyi has been placed in the synonymy of *C. jamesonii*, a South American species known also from Costa Rica. *Campylopus jamesonii* is characterized by interior basal cells enlarged and firm-walled but not porose, marginal cells at base not distinctly narrow and elongate, median and upper leaf cells quadrate, and leaf margins serrate in the upper 1/2. In contrast, *C. standleyi* has porose interior basal cells, narrower and elongate marginal cells at base (but not forming a hyaline border), oval to oblong median leaf cells, and leaf margins that are serrulate only at the apex.

Theriot (in correspondence to Bartram, FH) considered the median and basal cells of *C. standleyi* to fall within the variation he had noted for *C. jamesonii* in South America despite the fact that porose basal cells did not occur in South American material. He considered the two synonymous. My study of *C. standleyi* indicates that it differs from *C. jamesonii* not only in its porose interior basal cells but also in its leaves serrulate only at the apex and its firm-walled basal cells just above the alar cells (in *C. jamesonii* the basal cells above the alar cells are quadrate and lax-walled). The situation is complicated by the presence of collections such as Koch 5090 (NY, US) and Croat 32885 (MO) that 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.

The character states of *C. standleyi* place it intermediate to *C. jamesonii* and *C. subcuspidatus*. Until a more detailed study of the three taxa can be undertaken *C. standleyi* is here maintained at the species level.

24. *Campylopus subcuspidatus* (Hampe) Jaeg., Ber. Thatigk. St. Gallischen Naturwiss. Ges. 1870-71: 441. 1872. *Dicranum subcuspidatum* Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn 273. 1870. Type: Brazil, in vicinia Rio de Janeiro, Glaziou (not seen).

Campylopus praealtus (C. Müll.) Par., Ind. Bryol. Suppl. 96. 1900. *Dicranum praealtum* C. Müll., Hedwigia 37: 227. 1898. Type: Puerto Rico, Sierra de Luquillo, in cacumine summo montis Yunque inter fissuras rupium, Julio 1885, Sintensis (FH, NY).

Plants robust in dense, yellowish-green mats. Stems densely tomentose, up to 14 cm long, simple to sparingly branched, epidermal cells small and thick-walled. Leaves erect-patent to spreading-lanceolate, concave when wet, flattened when dry, narrowly acuminate, 8-10 mm long, denticulate at the apex, entire below. Upper cells elongate, incrassate, not porose, median cells elongate, 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 costae and frequently in excavate groups. Costae shortly excurrent, concolorous or at times hyaline at the extreme apex, up to 4/5 the leaf width at base, smooth to lightly mamillate at back; in cross-section guide cells well-developed, large ventral hyalocysts present, dorsal stereids well-developed. Setae 15-20 mm long. Capsules curved, furrowed when dry. Opercula conic-rostrate, 1.0 mm long. Calyptrae cucullate, entire at base.

Illustrations. Florschütz (1964, Fig. 19, a-i as *C. praealtus*).

Distribution in Central America. Belize (Stann Creek).

Habitat. Terrestrial over rock; 884 m.

Specimen examined.

BELIZE. Stann Creek: Molar Creek, Cockscomb branch of South Stann Creek, Cockscomb Mountains, Stevenson 3 (F, FH).

Until recently (Frahm, 1981) *C. subcuspidatus* was known in the Caribbean region as *C. praealtus*. The species is not common in Central America, and most collections named *C. subcuspidatus* are instead *C. standleyi*. Both are robust species with porose leaf cells and broad costae (up to 4/5 the leaf width) that are flattened when dry giving the leaves a distinctive appearance. There are two other large species in Central America with flattened leaves when dry (*C. jamesonii* and *C. heterostachys*) that may be confused with *C. subcuspidatus*. These two species, however, do not have porose leaf cells.

In *C. subcuspidatus* all of the basal cells and most of the median leaf cells are porose, the alar cells bulge outward in excavate groups, the leaves have a marginal hyaline border of long narrow cells at base and the upper leaf cells are elongate. In *C. standleyi* only the basal cells near the costa are porose, the alar cells, although well-developed, do not bulge outward in excavate groups, the marginal leaf cells, although they may be narrow and elongate, are not hyaline and

the upper leaf cells are oval.

25. *Campylopus surinamensis* C. Müll., *Linnaea* 21: 186. 1848. Type: Suriname, Kegel 516 (not seen).

Campylopus gracilicaulis Mitt., *J. Linn. Soc., Bot.* 12: 83. 1869. Type: Brazil, Fl. Negro, Spruce 60 (NY); Fl. Amazons, Santarem, Spruce 60b (NY).

Campylopus costaricensis Bartr., *Contr. U.S. Nat. Herb.* 26: 62. 1928. Type: Costa Rica, Limon, Finca Montecristo, on Rio Renventazon below Cario, Standley & Valerio, 48579 (holotype FH, isotype US). *syn. nov.*

Plants medium sized, forming loose tufts, yellowish to bright green. Stems variously tomentose, up to 3.5 cm long, branches few and irregularly spaced, epidermal cells small, firm-walled, dark red. Leaves typically spreading at base, becoming abruptly appressed to the stem, then crowded and spreading in apical comal tufts; leaves exceedingly variable in shape: basal leaves oblong-ovate, acute, up to 3 mm long, concave, margins inflexed, serrate at apex, not bordered by elongated cells; upper leaves linear-lanceolate, concave, acute, up to 2-4 mm long, serrate or entire not bordered by elongated cells. Costae percurrent in basal leaves, excurrent 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 laminal 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. "Setae about 7 mm long, bent at the middle or very strongly curved, especially when moist, often erect and spirally contorted when dry. Capsule ovoid, striate when dry, about 1.25 mm long and 0.5 mm wide, slightly scabrous at base. Peristome teeth 0.46 mm high, forked half way down, basal part finely, vetrically striate, the slender forks finely papillose. Lid conic-rostrate. Calyptra cucullate, ciliate at base." (Florschütz,

1964).

Illustrations. Bartram (1928, Fig. 5); Florschütz (1964, Fig. 22); Frahm (1978, Pl. 26); Frahm (1980, Fig. 10; Crum and Anderson (1981, Figs 97A-E, 98G-K, 99A-G).

Distribution in Central American. Belize (Orange Walk, Toledo); Costa Rica (Limon).

Habitat. On tree and tree stumps; 25-800 m.

Specimens examined.

BELIZE. Orange Walk: ca 3 km S of August Pine Ridge, 17°57'N; 88°44'W, Davidse & Brant 32733 (MO); Toledo: Monkey River, Swasey Branch, Gentle 3840 (F, NY, US).

COSTA RICA. Limon: Finca Montecristo, on the Rio Reventazon below Cairo, Standley & Valerio 48579 (FH, NY, US).

This species is broadly distributed (southeastern United States, throughout the Caribbean, Surinam and Brazil) and although we have seen material from only Belize and Costa Rica it is likely to be found throughout Central America. A report of the species from Honduras, (Frahm, 1981) is based upon a Belizian collection.

In its typical form *C. surinamensis* can be recognized by its distinctive habit: a short basal rosette of spreading leaves abruptly giving way to an elongated 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 of *C. surinamensis* can be exceedingly variable. Frahm (1980) described four types of leaves that can be found on a single plant and provided a discussion on leaf variability in *C. surinamensis*. When keying plants, leaves from stems bearing appressed leaves should be examined. In these leaves the alar cells are poorly developed, the costa excurrent, and the leaf margins distinctly serrate. Features important for the microscopic recognition of the species include its thin-walled, non-porose basal leaf cells and mamillate costae that in cross section have ventral hyalocysts usually smaller than the guide cells. It is this last feature that most clearly separates *C. surinamensis* from most other species of *Campylopus*. The only other species of

Campylopus in Central America with small ventral hyalocysts are *C. flexuosus*, *C. zygodonticarpus*, *C. oersteadianus*, *C. lamprodictyon*. and *C. pilifer*.

26. *Campylopus zygodonticarpus* (C. Müll.) Par., Ind. Bryol. 265. 1894. *Dicranum zygodonticarpum* C. Müll., Linnaea 42: 471. 1879. Type: Venezuela, Fendler 35 (isotype NY).

Dicranum donnellii Aust., Bot. Gaz. 4: 150. 1879. *Campylopus donnellii* (Aust.) Lesq. & James, Man. Mosses No. Amer., p. 79. 1884. Type: U.S.A., Florida, Austin Musci Appalachiani 470, Smith s.n. (MO). *syn. nov.*

Dicranum tuerckheimii C. Müll., Bull. Herb. Boissier 5:186. 1897. *Campylopodium tuerckheimii* (C. Müll.) Broth., Nat. Pflanzenfam. 1(3): 312. 1901. Type: Guatemala, Alta Vera Paz, in truncis arborum prope Coban, Tuerckheim 6652. (isotype NY). *syn. nov.*

Campylopus sargii Roll., Bull. Soc. Roy. Bot. Belgique 38: 8. 1900. Type: Costa Rica, Juan Vinas, 3400 ft., Sarg s.n. (isotypes NY, US). *syn. nov.*

Plants small, tufted, green to yellow-green. Stems variably tomentose, 1.0-3.0 cm long, epidermal cells small, firm walled. Leaves 2.5-6.0 mm long, erect at base, flexuous above when dry, concave, lanceolate-subulate, apices long subulate, margins with a few teeth at the extreme apex or serrulate above, not bordered by elongated cells. Costae shortly excurrent, in cross-section 1/3 to 1/2 the leaf width, smooth or lightly ribbed at back, guide cells well developed, dorsal stereids present, ventral hyalocysts present, smaller than or a little larger than the guide cells. Basal leaf cells firm- or lax-walled, inner basal cells near costa enlarged, quadrate to shortly rectangularly contrasting strongly with the shorter, quadrate, outer basal cells; median and upper leaf cells quadrate to rectangular, thick-walled not porose; 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 to 2/3 their lengths. Opercula shortly rostrate, 1.0 mm long.

Calyptrae cucullate, 1.5 mm long, variously fringed at base, at times fringed and unfringed in same collection.

Illustrations. Frahm (1978, Pl. 31).

Distribution in Central America. Guatemala (Alta Verapaz, Baja Verapaz, Quezaltenango, Quiche). El Salvador (Santa Ana); Honduras (Comayagua). Costa Rica (Alajuela, Cartago, Guanacaste, Heredia, San Jose). Panama (Bocas Del Toro, Chiriqui, Cocolé).

Habitat. Tree trunks and branches, rotting logs, humus at base of stumps, wet soil banks and cliffs; 950-2650 m.

Selected specimens examined.

GUATEMALA. Alta Verapaz: between Tactic and the divide on road to Tamahu, Standley 90784 (F, NY); Baja Verapaz: Civiya, Sharp 5191 (F); Quezaltenango: Volcan de Zunil, vicinity of Fuentes Georginas, Standley 85913 (F, US); Quiche: above Nebaj, Sharp 2535 (MO).

EL SALVADOR: Santa Ana: Los Planes del Monte Cristo, Watson 60 (MO).

HONDURAS. Comayagua: El Achote, near Siguatepeque, Standley 56117 (F, NY, US).

COSTA RICA. Alajuela: San Ramon, Brenes 21861 (F); Cartago: La Fuente, falda del Turrialba, Alfaro s.n. (F); Guanacaste: Tierras Morenas, Tilaran, Alfaro 24 (F); Heredia: Cerros de Zurqui, NE of San Isidro, Standley & Valerio 50485 (NY, US); San Jose: 8.5 km E of road to La Cima, 9°40'N; 83°51'W, Stevens 13426 (MO).

PANAMA. Bocas Del Toro: Cerro Colorado, just N of the Continental Divide, Allen 5337 (MO); Chiriqui: Cerro Colorado, just S of the Continental Divide, Allen 5385A (MO); Cocolé: vicinity of La Mesa trail to summit of Cerro Gaital, 8°37'N; 80°07'W, McPherson (MO).

Campylopus zygodonticarpus is a small plant with erect capsules and setaceous leaves that are erect at base and flexuous above when dry. The species is marked by four features, basal leaf cells that are enlarged, and firm-walled juxtacostally but smaller and firm-walled at the margins, ventral hyalocysts in the costa that are smaller than or only as large as the guide cells, poorly developed, frequently fugacious alar cells, and fringed calyptrae. Unfortunately, these characters are extremely variable. Thus, depending upon which

leaves are examined from a single collection 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 likewise variable. Both fringed and unfringed calyptrae have been seen in a single collection. Microscopically, only leaves from the erect portions of the stems should be examined.

Campylopus donnellii is treated here as a synonymy of *C. zygodonticarpus* rather than *C. surinamensis* (see Frahm, 1980 and Crum and Anderson, 1981 for opposing views). All three taxa are similar in having ventral hyalocysts in the costa that are smaller than or equal to the guide cells. In *C. donnellii* and *C. zygodonticarpus*, however, the basal cells near the costa are enlarged, quadrate, usually firm-walled and differentiated from the outer basal cells. In *C. surinamensis* the basal cells are uniform throughout. *Campylopus donnellii* has never been found with sporophytes. Since *C. zygodonticarpus* has erect capsules and *C. surinamensis* has curved capsules it may be that a definitive placement of *C. donnellii* will have to await the discovery of its sporophytes. Both *C. donnellii* and *C. zygodonticarpus* were described in the same year. I have chosen the epithet *zygodonticarpus* for the combined taxon because its type collection has sporophytes and calyptrae.

In southeastern North America and in the Caribbean this species has been confused with *C. gracilicaulis* Mitt. Although *C. gracilicaulis* is a slender plant, its leaf characters agree with those of *C. surinamensis*. Mitten described the capsules of *C. gracilicaulis* as erect, but the type material has capsules curved to inclined as in *C. surinamensis*. The calyptrae in the type material of *C. gracilicaulis* are ciliate.

Campylopus zygodonticarpus appears to be fairly common in Central America. Bartram (1949) confused this species with *C. flexuosus* and as a consequence most collections of *C. zygodonticarpus* from Central America have been named *C. subleucogaster* or *C. flexuosus*.

Campylopus tuerckheimii was treated as a synonymy of *Microcampylopus curvisetus* by Giese and Frahm (1985). However, the presence of ciliate calyptrae, weakly developed alar cells, quadrate lower leaf cells, and small ventral hyalocysts in the costae place *D. tuerckheimii* in the synonymy of *C. zygodonticarpus*.

Acknowledgements

I thank Alan T. Whittemore and Jan-Peter Frahm for their comments and opinions on the genus *Campylopus*; Robert E. Magill provided essential technical assistance with the manuscript.

Literature Cited

