

The paraleucobryoid *Campylopus* complex (Leucobryaceae) in South American páramos

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Abstract: The paraleucobryoid *Campylopus* complex consists of a small group of Andean species distinguished by a leaf cross section identical to that of *Paraleucobryum*. The complex differs from *Paraleucobryum* only in having cygneous rather than erect setae and capsule stomata absent rather than present. Here we treat four species, only two of which have previously been recognized in *Campylopus*. They are *C. albidovirens* Herzog, *C. pittieri* R.S.Williams, *C. densifolius* (Thér.) B.H.Allen & W.R.Buck, *comb. nov.* and *C. ochyriorum* B.H.Allen & W.R.Buck, *sp. nov.* A key is given to the four species; the two nomenclatural novelties are described in detail and illustrated.

Key words: *Campylopus*, paraleucobryoid complex, páramos, Anden South America, *Campylopus ochyriorum*, *sp. nov.*, *Campylopus densifolius* *comb. nov.*

Introduction

Campylopus Brid., with about 161 species (Crosby *et al.* 2000) is one of the largest genera of mosses with a world-wide distribution. Frahm (1988, 1990) maintained the genus originated in the Southern Hemisphere along the south coast of Gondwanaland. This seems plausible as judged by the presence of 65 *Campylopus* species in the Neotropics (Frahm 1991) and 50 species in Africa (Frahm 1985). The genus is taxonomically complex and plagued by attributes that add considerable difficulty to the group. For example, the primary distinguishing features of the genus (estomate capsules and sinuose setae when wet) are sporophytic, but the genus is dioicous and sporophytes are not often encountered. Even the value of these distinguishing features is questionable (Frahm 1983). For example, the sinuose seta seems to have evolved multiple times in the family as evidenced by its presence in several closely related genera as well as in more distantly related genera (*e.g.*, *Dicranoweisia* Lindb. ex Milde). In addition, the presence of generic pairs that are gametophytically nearly identical yet differ in the condition of their setae (*Atractylotropis* Mitt.–*Dicranodontium* Bruch & Schimp.; *Dicranella* (Müll.Hal.) Schimp.–*Campylopodium* (Müll.Hal.) Besch.; *Paraleucobryum* (Limpr.) Loeske–*Campylopus* p.p.; *Pilopogon* Brid.–*Campylopus* p.p.) provides more evidence for the multiple evolution of this feature in the Dicranaceae. An additional complexity of the group arises from the fact that single *Campylopus* stems are morphologically variable in sometimes having distinct areas with spreading leaves, tightly appressed leaves, and/or comal-tufted leaves. The leaves from these different areas usually have distinctly different anatomical features.

The *Campylopus* leaf has a generalized morphology that helps to make the genus recognizable. In shape they are usually ovate-lanceolate to ovate-subulate and have exceptionally broad, single, percurrent to excurrent costae. The leaves have two distinctly different parts: an ovate base with as many as five distinct regions — alar cells; lower leaf margins; lower leaf interior area; upper leaf cells at transition between lower/upper margins; and upper leaf cells —and a narrow upper limb filled almost entirely by the costae. The five ovate base regions provide useful taxonomic features. Leaf alar regions can be absent, present but fugacious and usually disintegrated, and weakly fugacious or firm and usually present. However, Florschütz and Florschütz-de Waard (1974) found that some *Campylopus* species

lacking alar cells when collected, formed distinct alar cells when cultivated. Since these species have the genetic capability to produce alar cells under some conditions, the reliability of this character as a major diagnostic feature was questioned. Lower leaf margins in *Campylopus* sometimes form a distinct border of very long, narrow cells. At other times, distinct limbidium-like borders are absent and the cells can be smaller, thicker-walled than the interior cells or they may be more or less homogeneous with the interior cells. The lower leaf interior area can have greatly enlarged, thin-walled, hyaline cells or somewhat enlarged firm- to thick-walled or even porose, colored cells. The upper leaf cells at the transition between the lower and upper margins are well differentiated, more or less consistent in shape, and rarely porose. The upper leaf cells are usually restricted to a very narrow band or in some cases they are absent because the costae occupy the entire upper part of the leaf. These cells have a tendency to be wildly variable in shape, *e.g.*, in a small area they can vary from quadrate to subrectangular to rhombic, rounded, oblong, or long-rhomboidal.

The structure of the *Campylopus* costa as seen in cross section has been considered a critical feature of the genus. As noted by Florschütz and Florschütz-de Waard (1974), Limpricht (1886) first subdivided the genus on this basis: subg. *Pseudocampylopus* Limpr. (no stereids, enlarged ventral hyalocysts, other cells with chlorophyll); subg. *Campylopus* (dorsal stereids); subg. *Palinocraspis* Limpr. (ventral and dorsal stereids). However, these seemingly clear-cut distinctions are considerably blurred by the recognition of intermediate cells (termed pseudostereids or substereids) and the observation that costal structure varies considerably from leaf insertion to apex (Thériot 1938). Indeed, based on the complete integration between stereid and pseudostereid development within single leaves as well as between *Campylopus* species it is generally recognized that the use of costal cross section anatomy in subdividing the genus is highly questionable (Florschütz & Florschütz-de Waard 1974, Frahm 1983, Robinson 1967).

Nevertheless, on a strictly pragmatic basis — *i.e.*, subdividing the genus into manageable units for identification purposes — we have found the following costal anatomy variation to be useful in designating groups: group 1, greatly enlarged ventral (adaxial) hyalocysts present; group 2, ventral hyalocysts moderately enlarged, equal to or smaller than guide cells; group 3, ventral stereids present; group 4, ventral hyalocysts or stereids absent, guide cells superficially exposed; group 5, dorsal (abaxial) mammillae or lamellae present; group 6, stereids absent, ventral and dorsal hyalocysts greatly enlarged, guide cells greatly reduced and chlorophyllose.

Although group 6 in the above list could refer to subg. *Pseudocampylopus* (Limpricht 1886), that ill-defined subgenus is plagued by the inclusion of *Campylopus* species with variously developed pseudostereids. Rather, as treated here this group refers to a very small cluster of species nearly restricted to South American páramos. The complex can be designated the *Campylopus* paraleucobryoid complex because their leaves in cross section are identical to those of *Paraleucobryum* species. Indeed, this complex differs from *Paraleucobryum* only in sporophytic (setae cygenous vs. erect; stomata absent vs. present) features. The costae in this complex are exceedingly broad, occupying $\frac{7}{8}$ of the leaf base. At or just below the middle of the ovate base the costae in cross section have greatly enlarged ventral hyalocysts in 1–3 layers, a median layer of small, quadrate chlorocysts, enlarged dorsal hyalocysts in 1–3 layers, and a cluster (3–5) of small, dorsal firm-walled cells at the middle of the cross section. In the subulate part of the leaf, cross sections have greatly enlarged ventral hyalocysts in one layer, a median layer of small, quadrate chlorocysts, and a dorsal layer with somewhat enlarged dorsal hyalocysts cells alternating with small chlorophyllose cells. In all but one member of the complex the dorsal chlorocysts form well-developed mammillae or 2-celled lamellae. Additionally, in those species with mammillae or lamellae the dorsal chlorocyst cells are positioned opposite the median chlorocyst cells. In contrast, the single member of the group

with dorsally smooth costae (*C. ochyriorum*) has dorsal chlorocyst cells alternating with the median chlorocyst cells. The leaves in all members of this complex have fugacious alar cells. Typically, the alar cells in even the youngest leaves are almost completely disintegrated. However, the leaves of *C. ochyriorum* have moderately fugacious alar cells. In this species the alar cells are more or less intact, but the cells along the upper margins, *i.e.*, in the transition areas between the alar cells and the basal leaf cells, are usually fragmented.

The *Campylopus* paraleucobryoid complex consists of five species of which four are treated here. The fifth member of the complex is an undescribed species nearly restricted to Ecuador. It will be described and illustrated in a future paper. Sporophytic features are known for only 2 of these species (*C. albidovirens* and *C. pittieri*). In both species the setae are cygneous and the capsules lack stomata. Since the sporophytic features of the other three species are not known, it remains uncertain whether they belong in *Campylopus* or *Paraleucobryum*. These species are here placed in *Campylopus* because their gametophytes closely resemble those of *C. albidovirens* and *C. pittieri*; they have exceptionally broad costae that are flattened at base when dry; and they are found in South American páramos. *Paraleucobryum* has never been collected in that habitat.

It is difficult to fully appreciate the magnitude of the confusion surrounding the *Campylopus* paraleucobryoid complex. At the beginning of this study there were 103 collections of the complex in the MO herbarium; nearly every one of these collections was misnamed; 43% of them did not even belong in the complex. There are two explanations for this confusion. First, the only comprehensive treatment of South American *Campylopus* (Frahm 1991) used solely the presence or absence of alar cells to separate *C. albidovirens* (alar cells present) from *C. pittieri* (alar cells absent). However, in both species the alar cells are strongly fugacious and hardly ever or never present. As a result, the name *C. pittieri* has been greatly over-applied. Secondly, most collections not belonging in the complex represent a group of species with enlarged inner basal cells and pseudostereid cells in their costae. This pseudostereid group of species is exceedingly difficult to distinguish from the *Campylopus* paraleucobryoid complex without prior experience with the group or access to reliably named comparative material. We cannot emphasize enough how difficult this complex is to accurately identify to species. Good quality leaf cross-sections are required from both the upper and lower parts of the leaf.

Results

Taxonomy

Key to the *Campylopus* paraleucobryoid complex

1. Leaves 4–7 × 0.5–1.2 mm; alar cells weakly fugacious, usually present; dorsal costal surface smooth above mid-leaf; median and dorsal chlorocysts alternating in upper part of leaf.....**3. *C. ochyriorum***
1. Leaves 3–10 × 0.8–1.5 mm; alar cells strongly fugacious, nearly always disintegrated; dorsal costal surface 1- or 2-celled mammillose above mid-leaf; median and dorsal chlorocysts opposite in upper part of leaf**2**
 2. Plants small; leaves 3–6 mm long; leaf apices smooth to weakly serrulate; costae narrowed at base to insertions..... **4. *C. pittieri***
 2. Plants medium-sized; leaves 6–10 mm long; leaf apices strongly roughened to toothed; costae straight at base to insertions.....**4**
3. Leaves setaceous, 1.0–1.2 mm wide at base; basal/upper transition cells irregularly oval to quadrate, not porose; dorsal and ventral hyalocysts at leaf base 1-layered **1. *C. albidovirens***
3. Leaves gradually acuminate, 1.2–1.5 mm wide at base; basal/upper transition cells elongate-oblong, porose; dorsal and/or ventral hyalocysts at leaf base 1–3-layered **2. *C. densifolius***

1. *Campylopus albidovirens* Herzog

Biblioth. Bot. 87: 19. 1916. Protologue. [Bolivia] In einer Quellwiese an der Waldgrenze über Tablas zwischen Gras und Sphagnum Polster bildend, ca. 3400 m, [Herzog] No. 2782.

TYPE. Bolivia, über Tablas, 3400 m. Leg. Herzog No. 2782, May 1911 (NY, isotype).

ILLUSTRATIONS. Herzog (1916, Pl. 1, Fig. 12); Frahm (1991, Fig. 21); Churchill & Linares-C. (1995, Fig. 60 a–e).

HABITAT. On damp banks, ravines; soil, humus and rocks in subalpine forests and páramos; 3300–4094 m.

SPECIMENS EXAMINED. **VENEZUELA.** Mérida: *Griffin 018906* (MO). COLOMBIA. Antioquia: *Churchill et al. 13376* (MO, NY), *MacDougal et al. 4529* (MO); Boyacá: *Cleef 1983* (MO), *Cleef 6765* (MO, NY); Caldas: *Churchill et al. 16325* (MO, NY); Cundinamarca: *Allen 10000* (MO, NY), *Cleef 3392* (MO), *Davidse & Gentry 5538* (MO, NY), *Frahm* [Campylopodexsiccatae 134, as *C. pittieri*] (MO, NY), *Frahm* [Campylopodexsiccatae 147, as *C. pittieri*] (MO, NY), *Linares & Churchill 3902* (MO, NY); Nariño: *Muñoz 98-272* (MO, NY). **ECUADOR.** Carchi: *Toapanta & Paredes 1681, 1682* (both MO); Cotopaxi/Pichincha: *Frahm & Gradstein* [Campylopodexsiccatae 138, as *C. pittieri*] (MO, NY). **PERU.** Cajamarca: *Hegewald & Hegewald 6200* (MO). **BOLIVIA.** La Paz: *Lewis 88-1496* [Bryophyta Neotropical Exsiccata 357, as *C. pittieri*] (MO, NY).

Campylopus albidovirens is a medium-sized plant, typically glaucous-green to greenish yellow in color. It has long (6–10 mm) setaceous, stiffly erect leaves that are 1.0–1.2 mm wide at base. Contrary to previous reports (Frahm 1991) the alar cells are strongly fugacious and nearly always disintegrated. The costae are not narrowed to the insertions; the basal transition cells are irregularly oval to quadrate and smooth; and the interior basal cells are well developed. Costal cross sections at midleaf have one layer of dorsal and one layer of ventral hyalocysts, above midleaf there are well-developed, 1–2-celled mammillae or lamellae that appear in surface view as projecting teeth. The upper leaf margins are sharply toothed. In cross sections above midleaf the median and dorsal chlorocysts are opposite one another.

2. *Campylopus densifolius* (Thér.) B.H.Allen & W.R.Buck, *comb. nov.*

Paraleucobryum densifolium Thér., Rev. Bryol. Lichénol. 11: 64. 1938 [1939]; *Bizotia densifolia* (Thér.) R.B.Pierrot, Rev. Bryol. Lichénol. 40: 27. 1974. Protologue. [Colombia] Paramo el Boqueron, bei Bogota, 3.500 m., leg. C. Troll., n^{os} 2.144, 2.145.

Plants medium-sized, compactly tufted, pale-green or yellowish green above, brownish below. Stems 2–8 cm high, erect, simple or forked, terete-foliate, moderately red-tomentose below; stems in cross section with $\pm$ enlarged outer cells, small, red, firm-walled cortical cells, central strand large, well developed, cells hyaline, thin-walled. Axillary hairs 5–7 cells long, basal 1–2 cells quadrate to short-rectangular, upper 4–5 cells oblong-cylindrical, all cells light reddish. Leaves crowded, equally foliate, erect when dry, erect-spreading when wet, concave throughout, ovate at base, gradually narrowed to long, slender acumina, 6–10 mm long, 1.2–1.5 mm wide below midleaf, lamellose-ribbed and serrate at back in upper half; margins erect below, subtubulose above, unistratose, entire below, strongly roughened to toothed at apices; costae filling $\frac{7}{8}$ of the leaf base, slightly excurrent, denticulate at apices; costal cross section at base with greatly enlarged ventral (adaxial) hyalocysts in 1–3 layers, a median layer of small, quadrate chlorocysts, moderately enlarged dorsal (abaxial) hyalocysts in 1–3 layers, and a small cluster of firm-walled dorsal cells at the middle of the cross section; costae in upper $\frac{1}{2}$ – $\frac{3}{4}$ mammillose to lamellose at back, mammilla/lamella cells chlorophyllose, in cross section ventral hyalocysts in 1-layer, median chlorocysts in 1-layer, and smaller dorsal hyalocysts in 1-layer, dorsal hyalocysts alternating with dorsal mammilla/lamella chlorocysts, median chlorocysts opposite dorsal mammilla/lamella chlorocysts; mammilla/lamella chlorophyllose cells spherical in surface view, toothed above; alar cells fugacious and usually disintegrated, remnant cells inflated, reddish to hyaline; inner basal cells enlarged, bulging, thin-walled, rectangular to subquadrate, $50\text{--}110 \times 20\text{--}37 \mu\text{m}$, outer basal cells forming border of 4–7 rows of long, narrow, firm-walled cells, $85\text{--}175 \times 5\text{--}8 \mu\text{m}$; lowermost upper basal cells short, strongly porose; uppermost basal cells oblong or rounded-rectangular, $10\text{--}22 \times 5\text{--}7 \mu\text{m}$, thick-walled, not porose. Dioicous (?). Perichaetia not seen. Perigonia terminal on lateral branches; perigonal leaves orbicular below, abruptly narrowed to long, narrow acumina, 2.5–3.0 mm long; paraphyses numerous; antheridia narrowly cylindrical, 1 mm long. Sporophyte unknown.

ILLUSTRATIONS. Florschütz & Florschütz-de Waard (1975, Figs. 1–3); Thériot (1938, Fig. 17). Fig. 1 & 2.

HABITAT. On rocks and soil in páramo; 3200–3855 m.

SPECIMENS EXAMINED. **VENEZUELA.** Mérida: *León et al. 9702/DV* (MO), *Griffin & López PV-578* (MO, NY), *Griffin & López 924* (MO); Táchira: *Griffin et al. 671* (MO). **COLOMBIA.** Bogotá: *Piovano s.n.* (MO); Boyacá: *Cleef 1906* (MO); Cundinamarca: *Cleef 3285* (MO). **ECUADOR.** Loja: *Laegaard & Vicente 19122D* (MO), *Laegaard et al. 19298A, 19321B* (both MO).

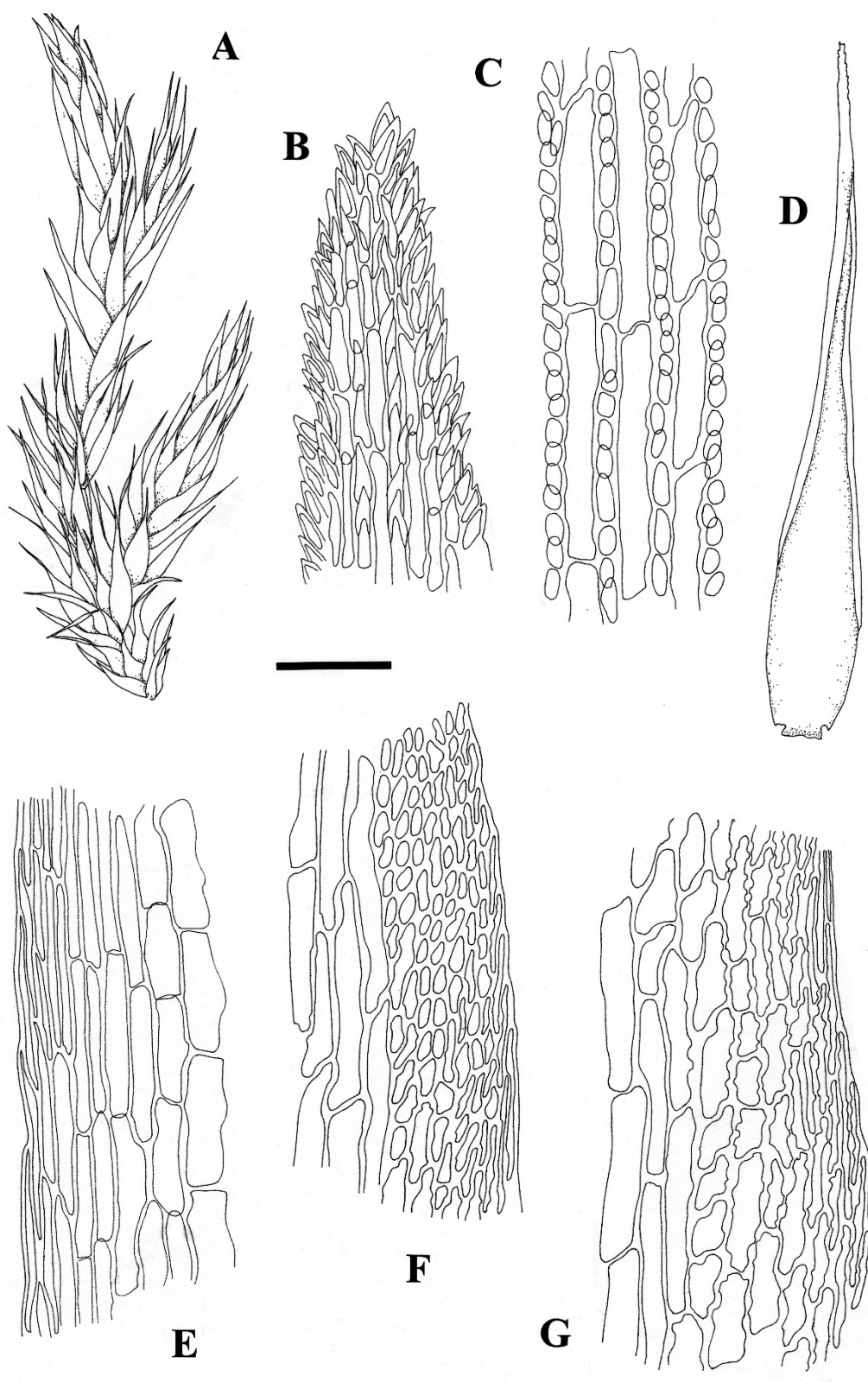


Fig 1: *Campylopus densifolius*. **A.** Habit. **B.** Leaf apex. **C.** Upper, dorsal costal surface, showing dorsal chlorocysts. **D.** Leaf. **E.** Basal leaf cells. **F.** Upper leaf cells. **G.** Leaf cells in transition area between upper/basal cells. Scale in mm: bar = 0.06 (B, C, E, F, G); bar = 1.25 (D); bar = 6.4 (A). All figures from León et al. 9702/DV (MO).

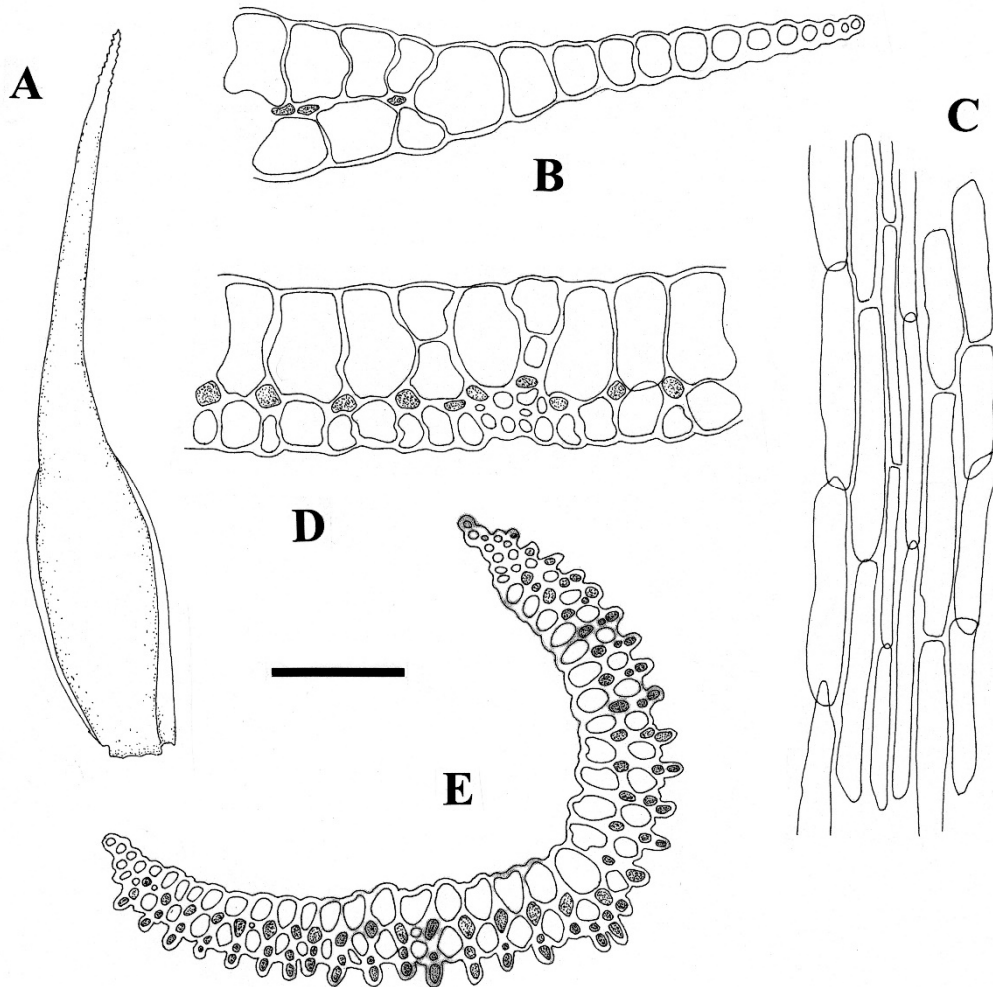


Fig 2: *Campylopus densifolius*. **A.** Leaf. **B.** Cross-section, middle of leaf base at margin. **C.** Dorsal mid-leaf surface showing median thick-walled cells. **D.** Cross-section, middle of leaf base showing median thick-walled cells. **E.** Cross-section, leaf apex. Scale in mm: bar = 0.06 (B, C, D, E); bar = 1.25 (A). All figures from León *et al.* 9702/DV (MO).

Campylopus densifolius is a medium-sized to robust, glaucous-green to greenish yellow plant. It has long (6–10 mm), gradually acuminate, stiffly to loosely erect leaves that are 1.2–1.5 mm wide at base. The alar cells are strongly fugacious and nearly always disintegrated. The costae are not narrowed to the insertions; the basal transition cells are elongate-oblong and strongly porose; and the interior basal cells are well developed. Costal cross sections at midleaf have 1–3 layers of dorsal and/or ventral hyalocysts, and above midleaf well-developed, 1–2-celled mammillae or lamellae that appear in surface view as projecting teeth. A curious aspect of the midleaf costal cross sections is the presence of a small cluster of firm-walled, dorsal cells at the middle of the cross section (Fig. 2 D). These cells are similar in position and somewhat reminiscent of the dorsal stereids seen in the costae of *Leucophanes* Brid. (Calymperaceae). In surface view on the dorsal side of the leaves (Fig. 2 C) they appear as a distinct morphological feature. In cross sections above midleaf the median and dorsal chlorocysts are opposite one another. An additional odd feature of *C. densifolius* is the presence of spherical chlorocysts as seen on the upper dorsal surface of the leaves (Fig. 1 C). These spherical chlorocysts are very similar in form to those of *Ochrobryum* Mitt. (Leucobryaceae), but in *C. densifolius* the chloro-

cysts are on the dorsal surface of the costae while those of *Ochrobryum* are in the median layer of the costae. The upper leaf margins are sharply toothed.

Previously, Florschütz & Florschütz-de Waard (1975) recognized that *Paraleucobryum/Bizotia densifolium/a* belonged in *Campylopus*. However, they considered it to be a synonym of *C. pittieri*, and thus did not make the new combination. Their illustration, although labeled as *C. pittieri*, appears to be *C. densifolius*.

3. *Campylopus ochyriorum* B.H.Allen & W.R.Buck sp. nov.

TYPE. Peru. Dept. Ancash, Prov. Yungay. Nahe der Laguna Llanganuco. Erde, Hoehe 4000–4035 m. Datum 17.10.1973. Leg. P. & E. Hegewald 7594 (MO, holotype; MO, NY, isotypes).

Plants medium-sized, compactly tufted, pale-green or yellowish green, brownish below. Stems 2–10 cm high, erect, simple or forked, terete-foliate, lightly red-tomentose below; stems in cross section with 2–3 layers of red, thick-walled sclerodermal cells, enlarged, red, thin- to firm-walled cortical cells, central strand large, well developed, cells hyaline, thin-walled. Axillary hairs 6–8 cells long, basal 1–2 cells quadrate to short-rectangular, light reddish or brownish, upper 5–6 cells oblong-cylindrical, hyaline. Leaves crowded, equally foliate, at times appearing somewhat comal-tufted due to terminal perigonia, erect when dry, erect to somewhat erect-spreading when wet, concave throughout, ovate at base, gradually narrowed to long, slender acumina, 4–7 long, 0.5–1.2 mm broad below midleaf, smooth at back in upper half, acute to rounded acute; margins erect below, subtubulose above, unistratose, entire below, entire to lightly serrate at apices; costae filling $\frac{7}{8}$ of the leaf base, percurrent, lightly toothed at apices; costal cross section at base with greatly enlarged ventral (adaxial) hyalocysts in 1 layer, median layer of small, quadrate chlorocysts, smaller dorsal (abaxial) hyalocysts in 1 layer, small cluster of firm-walled, dorsal, chlorophyllose cells at middle of cross section; costal cross section above smooth at back, ventral hyalocysts in one layer, median layer of chlorocysts, smaller layer of dorsal hyalocysts that alternate with 1 layer of dorsal chlorocysts, median chlorocysts alternating with dorsal chlorocysts; alar cells weakly fugacious, typically present, cells inflated, reddish to hyaline; inner basal cells below enlarged, bulging, thin-walled, rectangular, 40–80 × 12–23 μm , outer basal cells below forming border of 4–10 rows of long, narrow, 70–140 × 3–7 μm , firm-walled cells; upper basal cells irregularly subquadrate, rectangular to rounded-rectangular, 7–18 × 3–7 μm , thick-walled, not porose. Dioicous (?). Perichaetia not seen. Perigonia terminal on main stems; outer perigonial leaves ovate below, narrowly acuminate above, 3–4 mm long; inner perigonial leaves orbicular below, abruptly narrowed and broadly acute above, 1.0–1.5 mm long; paraphyses numerous; antheridia narrowly cylindrical, 1 mm long. Sporophyte unknown.

Campylopus ochyriorum is a large but slender, glaucous-green plant. It has fairly short (4–7 mm), gradually acuminate, erect leaves that are 0.5–1.2 mm wide at base. The alar cells are weakly fugacious and nearly always present, but with the upper cells in the alar/basal cell transition region often fragile. The costae are very broad below and straight to the insertions; the basal transition cells are irregularly subquadrate, rectangular to rounded-rectangular, smooth; and the interior basal cells are lax, thin-walled and well developed. Costal cross sections at midleaf have one layer of dorsal hyalocysts, one layer of ventral hyalocysts, and above midleaf the dorsal surface is smooth. The upper leaf margins are smooth to weakly serrate. The outstanding feature of this species is seen in leaf cross sections above midleaf. In this area the median chlorocysts alternate with the dorsal chlorocysts. In all other species of the *Campylopus* paraleucobryoid complex the median and dorsal chlorocysts are opposite one another.

ILLUSTRATIONS. Fig. 3.

HABITAT. On rocks and soil; 3100–4035 m.

ETYMOLOGY. This new species, long-confused, is named for Ryszard (Rysiek) Ochyra and Halina Bednarek-Ochyra, in honor of their work making sense of other taxonomically difficult groups.

SPECIMENS EXAMINED. PERU. Ancash: *Frahm* [Campylopodes Peruvianae Exsiccatae 1, as *C. albidovirens*] (MO, NY), *P. & E. Hegewald* 7534, 7595 (both MO), *López et al.* 8672a (MO); La Libertad: *E. Hegewald* 5949 (MO).

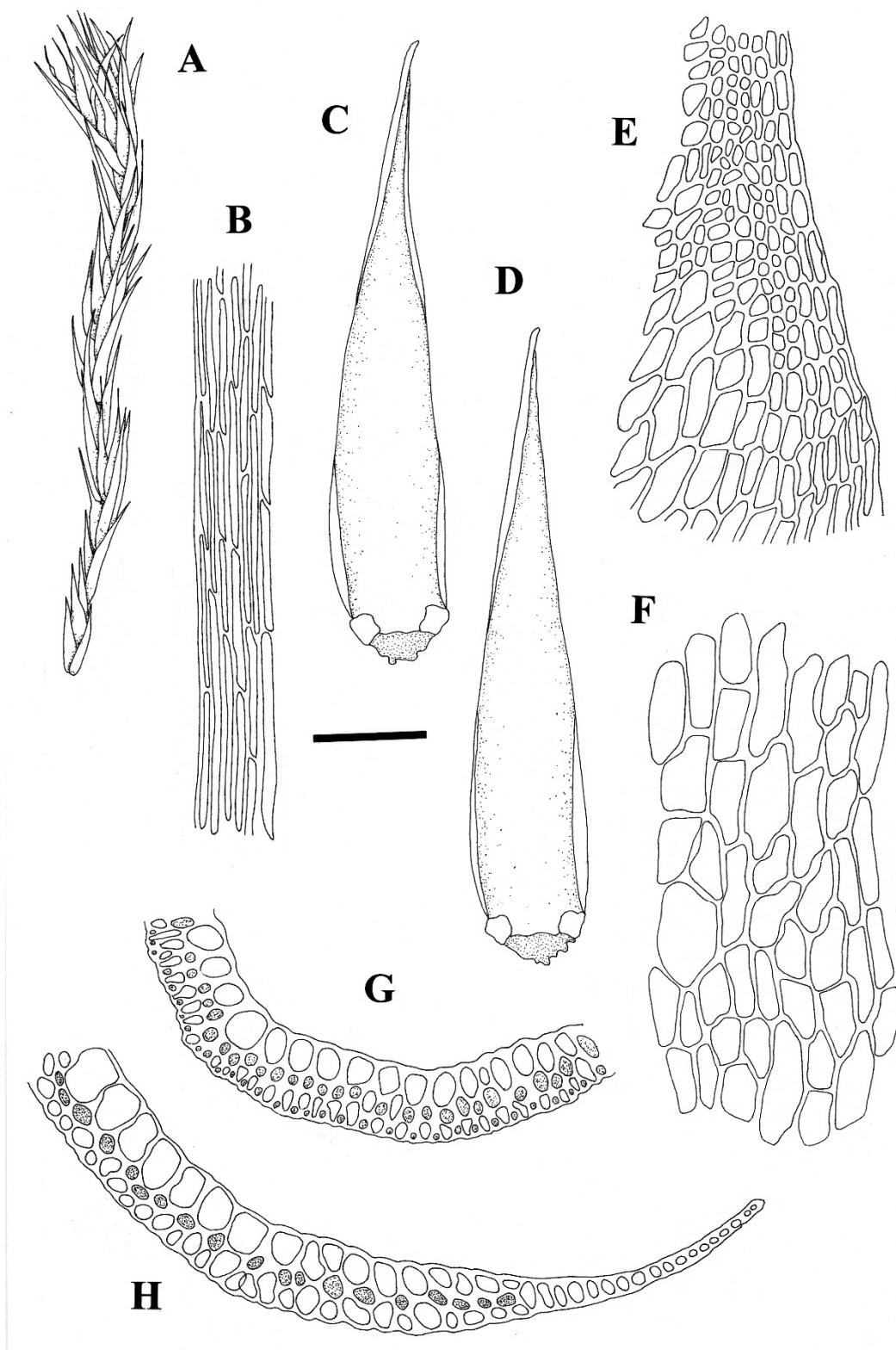


Fig 3: *Campylopus ochyriorum*. **A.** Habit. **B.** Basal leaf cells at margin. **C & D.** Leaves. **E.** Upper leaf cells. **F.** Inner basal leaf cells. **G.** Cross-section, leaf apex. **H.** Cross-section, middle of leaf base. Scale in mm: bar = 0.05 (G); bar = 0.06 (B, E, F, H); bar = 1.25 (C, D); bar = 1.2 (A). All figures from Hegewald & Hegewald 7594 (MO).

4. *Campylopus pittieri* R.S.Williams

Bull. Torrey Bot. Club 34: 569. 1907 [1908]. Protologue. [Colombia] Headwaters of Rio Lopez, Rio Palo basin, 2500–3000 meters, January 24, 1906, H. Pittier (1008). Type. Plants of Colombia. State of Cauca. Headwaters of Rio Lopez, Rio Palo basin, Tierra Adentro; alt. 2500–3000 m. No 1088 H. Pittier, Collector. January 24, 1906 (NY, isotype).

ILLUSTRATIONS. Churchill & Linares-C. (1995, Fig. 63 f–j); Frahm (1991, Fig. 2 A). Frahm (1991) Fig. 109 is *Campylopus nivalis* (Brid.) Brid.

HABITAT. On soil, rocks and branches in páramos; 3250–4900 m.

SPECIMENS EXAMINED. **VENEZUELA.** Mérida: *Schäfer-Verwimp & Verwimp 12081* (MO). **COLOMBIA.** Caldas: *Florschütz 4360* [*Campylopus Exsiccatae* 152] (MO, NY); Cundinamarca: *Cleef 3592* (MO), *Cleef & Jaramillo 4147* (MO, NY), *Ireland 23558* (MO, NY); Valle: *Churchill 15317* (MO, NY). **ECUADOR.** Pichincha: *Barclay & Luajibioy 8889* (MO). **BOLIVIA.** La Paz: *Lewis, 79-1929* (MO), *87240* (MO, NY), *87368* (MO, NY).

Campylopus pittieri is a small to medium-sized, often reddish yellow plant. It has fairly short (3–6 mm), gradually acuminate, stiffly erect leaves that are 0.8–1.0 mm wide at base. The alar cells are strongly fugacious and nearly always disintegrated. The costae are narrowed to the insertions; the basal transition cells are quadrate to short-oblong, smooth; and the interior basal cells are not as enlarged, lax, and thin-walled as other species in the complex. Costal cross sections at midleaf have one layer of dorsal, one layer of ventral hyalocysts, and above midleaf well-developed, 1–2-celled mammillae or lamellae that appear in surface view as projecting teeth. The upper leaf margins are smooth to weakly serrate. In cross sections above midleaf the median and dorsal chlorocysts are opposite one another.

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