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CAMPYLOPUS STEEREI (DICRANACEAE), A NEW PARALEUCOBRYOID SPECIES FROM SOUTH AMERICAN PÁRAMOS

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Abstract: The *Campylopus* paraleucobryoid complex, restricted to Andean South America, is discussed and a new species, *C. steerei*, is described. These plants differ from other members of the complex in having all dorsal (abaxial) surface cells with very thick, orange outer walls. Additionally, *Campylopus erratus* nom. nov. is provided to correct an earlier nomenclatural error. A key is included to separate the five species in the complex.

Keywords: *Campylopus*, paraleucobryoid species complex, páramos, Colombia, Ecuador, key to species

INTRODUCTION

A consensus on the number of moss species is difficult since new species continue to be described while others are newly synonymized. However, Crosby *et al.* (2000) provided a good approximation in recognizing 12760 moss species making it one of the largest plant groups outside the flowering plants. The genus *Campylopus* Brid. has a world-wide distribution and with about 161 species (Crosby *et al*. 2000) is one of the most speciose moss genera. There are about 65 *Campylopus* species in the Neotropics (Frahm 1991). The genus is taxonomically complex and has morphological features that add considerable difficulty in naming *Campylopus* collections. At the generic level the primary distinguishing features of the genus (estomate capsules and sinuose setae when wet) are sporophytic. But *Campylopus* is dioicous and collections often lack sporophytes. Moreover, there is no general agreement as to the taxonomic value of these distinguishing generic features (Frahm 1983). For example, sinuose

setae seem to have evolved multiple times within the family since they are present in several closely and distantly related genera. Certainly the presence of generic pairs in the Dicranaceae that are gametophytically nearly identical yet differ in the condition of their setae (*Atractylocarpus* Mitt.–*Dicranodontium* Bruch & Schimp.; *Dicranella* (Müll.Hal.) Schimp.–*Campylopodium* (Müll.Hal.) Besch.; *Paraleucobryum* (Limpr.) Loeske–*Campylopus p.p.*; *Pilopogon* Brid.–*Campylopus p.p.*) calls into question the taxonomic value of the feature in the family. At the species level, the presence in some *Campylopus* species of single stems that have distinct areas with leaves that are variably spreading, tightly appressed, and/or comal-tufted each with different associated morphological features causes considerable identification problems.

Nevertheless, *Campylopus* can usually be recognized by its generalized leaf morphology: often ovate-lanceolate to ovate-subulate leaves; single, percurrent to excurrent, exceptionally broad costae (often 1/2 to 7/8 the leaf width at base); and strongly differentiated, often inflated alar cells. The *Campylopus* leaf has two distinctly different parts. There is an ovate base with as many as five taxonomically important 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 best taxonomic features are usually found in the ovate basal regions. The leaf alar regions can be undifferentiated or variously differentiated. When differentiated, the alar cells can be firm or irregularly fugacious and often disintegrated. But, it is unclear how taxonomically reliable alar cell development is since some *Campylopus* species that lack alar cell development when collected can form distinct alar cells when cultivated (Florschütz and Florschütz-de Waard 1974). The 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 marginal cells are 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, sometimes porose, colored cells. The upper leaf cells at the transition between the lower and upper margins are often 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 and the costae occupy the entire upper parts of the leaves. When present the upper leaf cells are often distressingly variable in shape–nearly contiguous cells can be quadrate, subrectangular, rhombic, rounded, oblong, or long-rhomboidal.

The structure of the *Campylopus* costa as seen in cross section is a critical feature of the genus. In its simplest form the costa in cross-section consists of a central row of enlarged guide cells, a band of dorsal stereids and a band of ventral stereids. In most species the ventral stereids are replaced by thin-walled hyalocysts that can be greatly enlarged or more or less similar in size to the guide cells. Occasionally the ventral stereids or hyalocysts are absent and the guide cells are superficial, *i.e.*, ventrally exposed. In most *Campylopus* species the dorsal stereid band of the costa is well developed, but a few species have comparatively large, moderately thick-walled dorsal stereids termed pseudostereids or substereids. In addition, the dorsal surface of the costa can be variably ribbed or lamellose.

Limpricht (1886) was the first to subdivide *Campylopus* on the basis of costal variation: subg. *Pseudocampylopus* Limpr. (no stereid cells, enlarged ventral hyalocysts, guide cells with chlorophyll); subg. *Campylopus* (dorsal stereids present); subg. *Palinocraspis* Limpr. (ventral and dorsal stereids present). However, the distinctions between these subgenera are muddled by the presence of pseudostereids or substereids that represent intermediate cell types and the observation that costal structure can vary considerably from leaf insertion to apex (Thériot 1938). Indeed, because of the confusing intergradation between stereid and pseudostereid cell development within single leaves or between *Campylopus* species some authors (Robinson 1967; Florschütz and Florschütz-de Waard 1974; Frahm 1983) considered the use of costal cross section anatomy in subdividing the genus highly questionable.

Nevertheless, on a strictly pragmatic basis – *i.e.*, subdividing the genus into manageable units for identification purposes – costal anatomy variation is here considered useful and can be employed to divide *Campylopus* into six groups. Group 1, ventral hyalocysts present, considerably larger than guide cells. Group 2, ventral hyalocysts present, equal to or smaller than guide cells. Group 3, ventral stereids present. Group 4, ventral hyalocysts and ventral

stereids absent, guide cells superficially exposed. Group 5, dorsal (abaxial) mammillae or lamellae present. Group 6, ventral/dorsal stereids or pseudostereids absent, ventral and dorsal surface cells enlarged, guide cells reduced, guide cells and dorsal surface cells chlorophyllose.

As treated here Group 6 in the above list refers to a small, highly distinctive cluster of species nearly restricted to South American páramos. The group has been designated the *Campylopus* paraleucobryoid complex (Allen and Buck 2019) because their leaves in cross section are nearly identical to those of *Paraleucobryum* species. Indeed, this complex differs gametophytically from *Paraleucobryum* only in having costae with two (median and dorsal) layers rather than a single (median) layer of chlorocysts and often having mammillae or lamellae on the upper dorsal costal surface above midleaf. Absolute certainity as to whether or not collections with this costal anatomy belong to *Campylopus* or *Paraleucobryum* depends solely on sporophytic evidence: *Campylopus*, setae sinuose when wet, capsules lacking stomata; *Paraleucobryum*, setae straight when wet, capsules with stomata. The costae in the paraleucobryoid complex are exceedingly broad, usually occupying 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, a median layer of small, quadrate chlorocysts, enlarged dorsal hyalocysts, and a cluster of (3–5) small, dorsal stereid cells at the middle of the cross section. In the subulate part of the leaf the cross sections have greatly enlarged ventral hyalocysts in 1-layer, a median layer of small, quadrate chlorocysts, and a dorsal layer with somewhat enlarged dorsal hyalocyst cells usually alternating with small chlorophyllose cells. In most members 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 typically positioned opposite the median chlorocyst cells. In contrast, one member of the group with dorsally smooth costae (*C. ochyrarum*) 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. In one species of the complex (*C. ochyrarum*) the leaves have moderately fugacious alar cells. In this species while the alar cells are more or

less intact, the cells along the upper margins, *i.e.*, in the transition areas between the alar cells and the basal leaf cells, are usually fragmented.

While conducting a recent study of the paraleucobryoid *Campylopus* complex in South American páramos the authors encountered exceptionally robust (plants to 14 cm high, leaves to 11 mm long), high elevation (3642–4100 m) plants of *Campylopus* (sporophytes with estomate capsules and sinuose setae) from Columbia and Ecuador that belong in the paraleucobryoid complex. These plants further differed from other members of the paraleucobryoid *Campylopus* complex in having all dorsal (abaxial) surface cells with very thick, orange outer walls. These plants are described below as a new species in the *Campylopus* paraleucobryoid complex.

RESULTS

Campylopus steerei B.H.Allen & W.R.Buck, **sp. nov.** (*Figures 1, 2*)
Type: ECUADOR. Tungurahua Province, Cordillera de los Llanganates, Chinas Pass between Río Muyu and Río Golpe, 10.5 km NW of Cerro Hermoso; lake and boggy páramo. 1°10'S; 78°20'W, 4000 m; 8 November 1980, *L. Holm-Nielsen & J. Jaramillo 28055* (HOLOTYPE MO; ISOTYPE NY).

Description: Plants robust, compactly tufted, yellowish green or pale-green, brownish below. Stems 5–14 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, firm-walled cortical cells, central strand well developed, cells hyaline, thin-walled. Axillary hairs 5–8 cells long, basal 1–2 cells quadrate to short-rectangular, light reddish or brownish, upper 5–6 cells oblong-cylindrical, hyaline or light reddish. Leaves crowded, equally foliate, stiffly erect-appressed when dry, erect to lightly erect-spreading when wet, concave below, tubular concave above, ovate at base, gradually narrowed to long, slender acumina, 7–11 mm long, 1.0–1.5 mm broad below midleaf, smooth at back in upper half; margins erect below, subtubulose above, unistratose, entire throughout; costae filling 7/8 of the leaf base, percurrent, lightly toothed at apices, smooth at back; in cross section costae three layered, at midleaf with one row of greatly enlarged ventral (adaxial) hyalocysts, one row of small,

median chlorocysts and one row of small dorsal chlorocysts alternating with small dorsal hyalocysts and opposite median chlorocysts, all dorsal (abaxial) cells with very thick, orange outer walls; in lower part of leaf at middle of costal cross section with small cluster of dorsal, thick-walled cells; alar cells fugacious, typically absent even in youngest leaves; inner basal cells below enlarged, bulging, thin-walled, rectangular, 42–88 × 15–25 µm, transitioning toward the margin to long, rectangular strongly porose cells, outermost basal cells below forming border of 4–10 rows of long, narrow, firm-walled cells, 70–140 × 3–5 µm; upper basal cells rounded-rectangular to long, narrowly rectangular, or elongate-rectangular, thick-walled, porose or not; apical cells rounded-rectangular to narrowly elongate-rectangular. Dioicous, perichaetia terminal, perigonia not seen. Setae 15–20 mm long, cygneous, yellow becoming red with age. Capsules cylindrical, 1.5–2.0 mm long, ribbed when dry, neck tapered to setae; exothecial cells with 3–4 rows of small, thick-walled cells below mouth, lower cells long-rectangular, horizontal walls thin, vertical walls strongly collenchymatous; stomata absent; opercula long-rostrate, 1 mm long; annuli revoluble with 1–2 rows of vesiculose cells, upper row hyaline, lower row light reddish, deciduous; peristome teeth 16, inserted within capsule mouth, divided in upper 1/2–3/4, dorsal (outer) side deep red below bifurcation, yellowish at bifurcation, filaments hyaline, with thin, reddish orange, hardly projecting trabeculae, lamellae vertically papillose-striate, filaments papillose, ventral (inner) side with thick, dark-red, projecting trabeculae, lamellae smooth. Spores smooth, 15–20 µm. Calyptrae cucullate, 2.5–3.0 mm long, pale-yellow to reddish yellow, ciliate-fringed at base, fringe cells unicellular, 100–350 µm long.

Habitat: *Polylepis* forest, *Espeletia*, *Lachemilla*, *Loricaria, Neurolepis* and *Swallenochloa* páramos, epiphyte in elfin forest and on vertical rocks; 3620–4100 m.

Etymology: This new species is named for William Campbell Steere (1907–1989) who collected bryophytes in Colombia and Ecuador during the Cinchona Missions, 1942–1943.

Specimens examined: COLOMBIA. Nariño: *Delgado et al. 40*, (MO, NY). **ECUADOR**. **Carchi:** *Holm-Nielsen et al. 5862* (MO, NY); **Napo/Pichincha:** *Øllgaard et al. 34423* (MO, NY); **Napo:** *Holm-Nielsen 16452* (MO, NY), *Holm-Nielsen et al. 28221, 28242, 28754* (all MO, NY), *Løjtnant et al.11087* (MO, NY), *Øllgaard et al. 38737*

(MO, NY); **Tungurahua:** *Holm-Nielsen et al. 28024, 28048, 28055*, *28088, 28196, 28530, 28631* (all MO, NY).

KEY TO THE *CAMPYLOPUS* PARALEUCOBRYOID COMPLEX

1 Leaves 4–7 × 0.5–1.0 mm; alar cells weakly fugacious, usually present; dorsal costal surface smooth above mid-leaf; median and dorsal chlorocysts alternating in upper part of leaf..... ***C. ochyrarum*** B.H.Allen & W.R.Buck

– Leaves 3–11 × 0.8–1.5 mm; alar cells strongly fugacious, nearly always disintegrated; dorsal costal surface 1- or 2-celled mammillose or smooth 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..... ***C. pittieri*** R.S.Williams

– Plants medium-sized to robust; leaves 6–11 mm long; leaf apices strongly roughened to lightly toothed; costae straight at base to insertions..... **3**

3 Leaves setaceous, 1.0–1.2 mm wide at base; basal/upper transition cells irregularly oval to quadrate..... ***C. albidovirens*** Herzog

– Leaves gradually acuminate, 1.0–1.5 mm wide at base; basal/upper transition cells elongate-oblong, rectangular or elongate-rectangular..... **4**

4 Plants 2–8 cm high; costae lamellose-ribbed and serrate dorsally on upper half; leaves strongly roughened to toothed at apices; dorsal (abaxial) surface cells with weakly thickened, concolorous outer walls..... ***C. erratus*** B.H.Allen & W.R.Buck

– Plants 5–14 cm high; costae smooth dorsally on upper half; leaves lightly toothed at apices; dorsal (abaxial) surface cells with very thick, orange outer walls..... ***C. steerei*** B.H.Allen & W.R.Buck

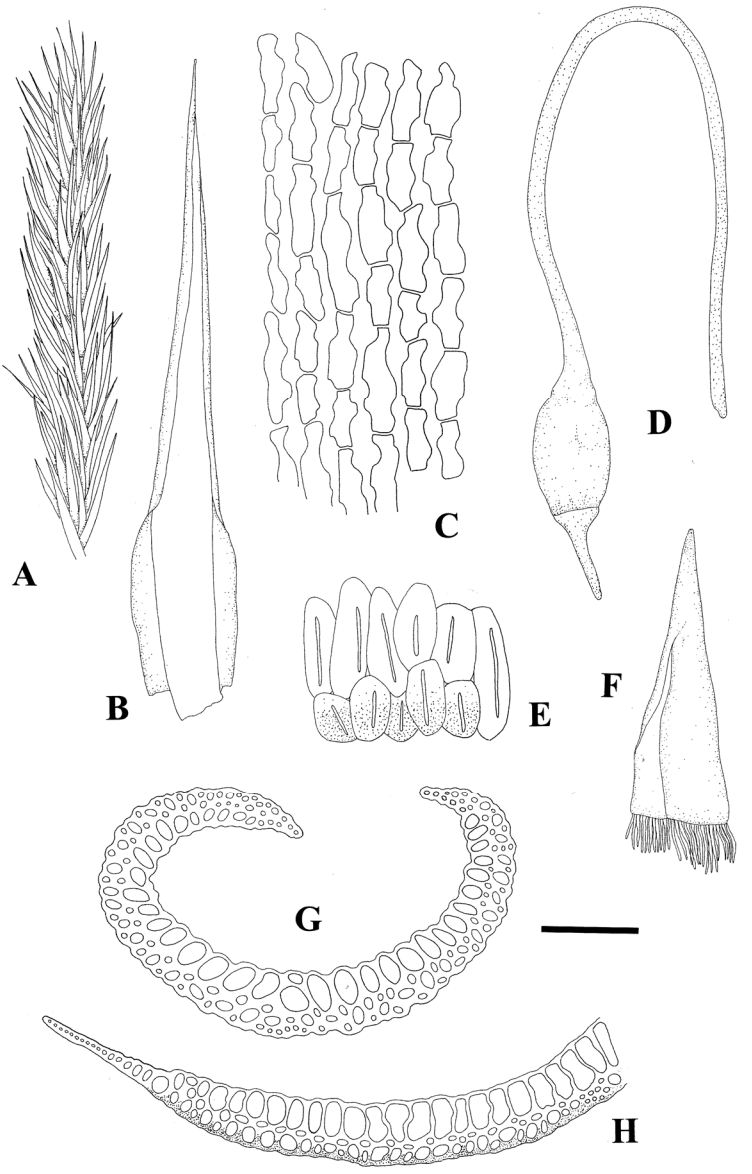

Figure 1. *Campylopus steerei*. **A**. Habit. **B**. Leaf. **C**. Exothecial cells at mid-capsule. **D**. Seta, capsule and operculum. **E**. Annulus. **F**. Calyptra. **G**. Cross section, upper part of leaf. **H**. Cross section basal part of leaf. Scale in mm: bar = 0.05 (C, E, G); bar = 0.1 (H); bar = 0.8 (F) bar = 1.25 (B, D); bar = 8 (A); figures from A, B, G, H from *L. Holm-Nielsen & J. Jaramillo 28055* (MO), figures C, D, E, F from *Øllgaard 34423* (MO).

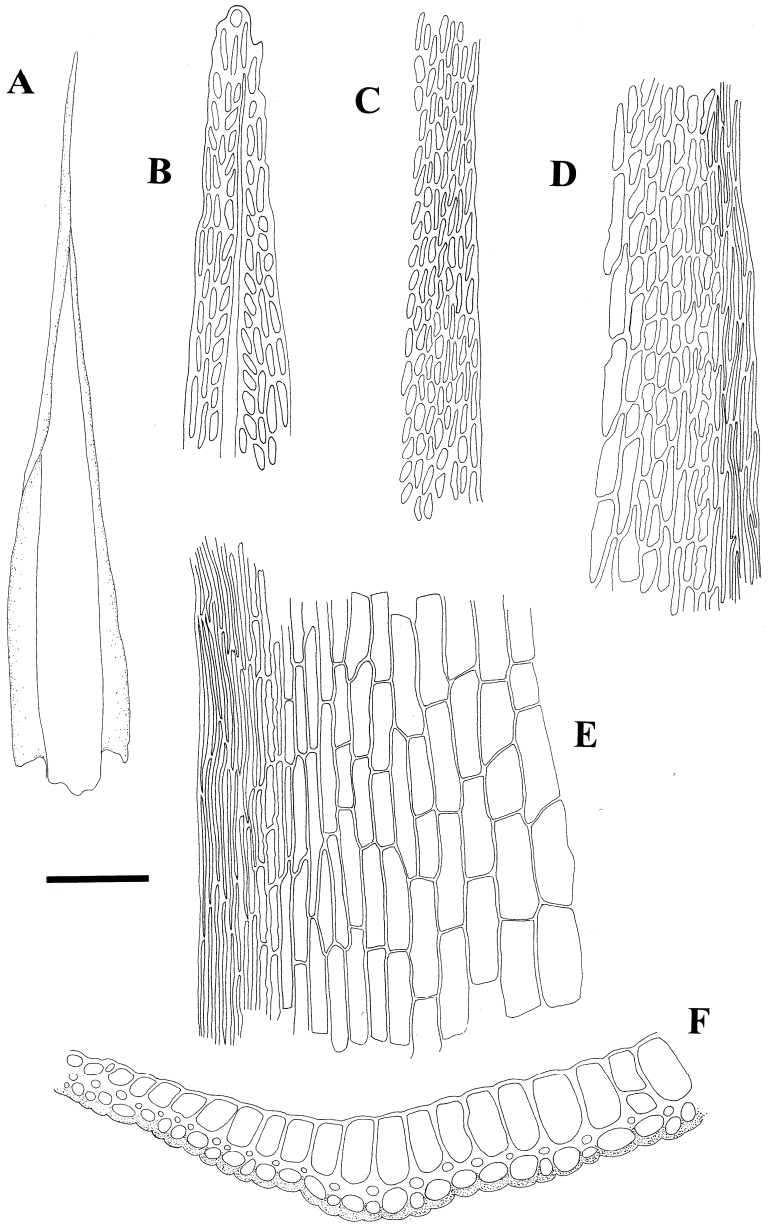

Figure 2. *Campylopus steerei*. **A**. Leaf. **B**. Leaf apex. **C**. Upper leaf cells and margin. **D**. Upper leaf cells at cellular transition area and margin. **E**. Basal leaf cells and margin. **F**. Cross section, midleaf. Scale in mm: bar = 0.05 (B, C, D, E, F); bar = 1.25 (A); all figures from *L. Holm-Nielsen & J. Jaramillo 28055* (MO).

Campylopus steerei is a robust plant, typically yellowish or pale-green in color. It has long (7–11 mm) ovate-lanceolate leaves that are 1.0–1.5 mm wide at base. The alar cells are fugacious and typically absent even in youngest leaves. The costae are not narrowed to the insertions; the basal transition cells are narrowly rectangular, or elongate-rectangular. In cross section the costae are smooth at back, three-layered at midleaf with one row of greatly enlarged ventral (adaxial) hyalocysts, one row of small, median chlorocysts and one row of small dorsal chlorocysts alternating with small dorsal hyalocysts and opposite median chlorocysts. The upper leaf margins are lightly toothed. In cross sections above midleaf the median and dorsal chlorocysts are opposite one another.

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. The alar cells are strongly fugacious and nearly always disintegrated. The costae are straight at base 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 1 layer of dorsal and 1 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.

Campylopus erratus 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 straight at base to the insertions; the basal transition cells are elongate-oblong, 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 have 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. We here take this opportunity to correct our multiple errors in naming this species:

Campylopus erratus B.H.Allen & W.R. Buck, *nom. nov.*
Paraleucobryum densifolium Thér., Rev. Bryol. Lichénol. 11: 64. 1939; *Campylopus densifolius* (Thér.) B.H.Allen & W.R.Buck, Acta Mus. Siles. Sci. Nat. 68: 98. 2019, *hom. illeg. non Campylopus densifolius* Ångstr., Öfvers. Kongl. Vetensk.-Akad. Förh. 29(4): 18. 1872; *Campylopus florschuetzianus* B.H.Allen & W.R.Buck, Evansia 38: 27. 2021, *nom. inval.*

Campylopus ochyrarum 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 mostly present, but the upper cells at the alar/basal cell transition region are usually 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 above midleaf have a smooth dorsal surface. The upper leaf margins are smooth to weakly serrate. In cross sections above midleaf the median/dorsal chlorocysts alternate with one another.

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 less enlarged, lax, and thin-walled than other species in the complex. Costal cross sections above midleaf have 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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