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## Studies on Colombian Cryptogams

### VII. Culture studies on the taxonomic relevance of costal anatomy in the *Campylopus leucognodes-subconcolor* complex and in *Campylopus pittieri*

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#### ABSTRACT

Observations on costal anatomy in Colombian material of the *Campylopus leucognodes-subconcolor* complex revealed a correlation between habitat humidity and degree of cell wall thickness. Cultivation experiments confirmed the assumption that the presence or absence of pseudostereids in this group is environmentally controlled. The taxonomic consequence of these findings makes us consider *C. leucognodes* (C. Müll.) Par. and *C. argyrocaulon* (C. Müll.) Mitt. synonymous with *C. subconcolor* (Hampe) Mitt.; the latter name is correct for the species in its new circumscription. Cultivation experiments on *Campylopus pittieri* Williams produced no effect on the observed variation in the costal cell-pattern, but cultivation seemed to suppress the development of apical ridges on the dorsal surface of the costa. The taxonomic value of the two varieties of *C. pittieri* is discussed.

#### *I. Campylopus leucognodes-subconcolor*

#### INTRODUCTION

The cross section of the leaf costa in typical *Campylopus leucognodes* (C. Müll.) Par. (type: Bolivia, *Germain s.n.*, NY) shows thick-walled cells and a dorsal band of small cells with narrow lumina. Consequently, *C. leucognodes* has been classified among species of the subgenus *Pseudocampylopus*, characterized by a dorsal costal band of "pseudostereids" (Thériot, 1939) or "stereids" (Robinson, 1967). The difference between pseudostereids and stereids is not sharp: "every possible intergradation of stereid and pseudostereid development seems to exist in the genus, and some species with different costal structure are almost certainly closely related" (Robinson l.c.: p.

12). Considerable variation in costal cell wall thickness and pseudostereid development in *C. leucognodes* was observed by Florschütz and Florschütz-de Waard (1974), who encountered great difficulties in distinguishing between *C. leucognodes* and *C. subconcolor* (Hampe) Mitt. (type: Colombia, Lindig 2013b, FH), a species supposedly differing from *C. leucognodes* by the thin-walled costal cells and the total absence of pseudostereids. Cross sections of both species show a costa with a ventral band of large cells and a dorsal pattern of transverse rows of two cells alternating with two smaller cells (figs. 1a and 2a). The alternation pattern is obscured in the centre of the costa where the smaller cells increase in number and at the costal margin where the rows of small cells are replaced by one larger cell. Florschütz and Florschütz-de Waard (l.c.) suggested that the observed variation in cell wall thickness and the absence or presence of pseudostereids in the *C. leucognodes-subconcolor* complex might be due to ecological circumstances. Culture experiments were set up to test this hypothesis. This paper presents the results of the experiments and evaluates the taxonomic status of the investigated species.

#### MATERIAL AND METHODS

Twenty specimens belonging to the *C. leucognodes-subconcolor* complex, from various ecological sites in the Colombian Andes (leg. P.A. Florschütz, Sept./Oct. 1972; COL, U), were cultivated for two years under controlled light- and temperature conditions in a growth-chamber, according to the cultivation method of Schelpe (1953). Stem tips were placed on coarse sand, washed with HCL (PH=5) and were kept saturated by regularly adding diluted Knop's solution (1/100 strength). The cultures were maintained throughout the experiments in closed glassboxes at a temperature of 15 °C, on a day-night cycle of 12–12 h. and at a lightintensity of 1000–1500 Lux.

After two years of cultivation the growing leafy shoots were harvested and costal anatomy characteristics were observed and drawn from hand-made sections. Drawings were made with the aid of a Wild-Heerbrugg drawing apparatus. The results were compared with drawings of the costal anatomy in dried field material of the same collections.

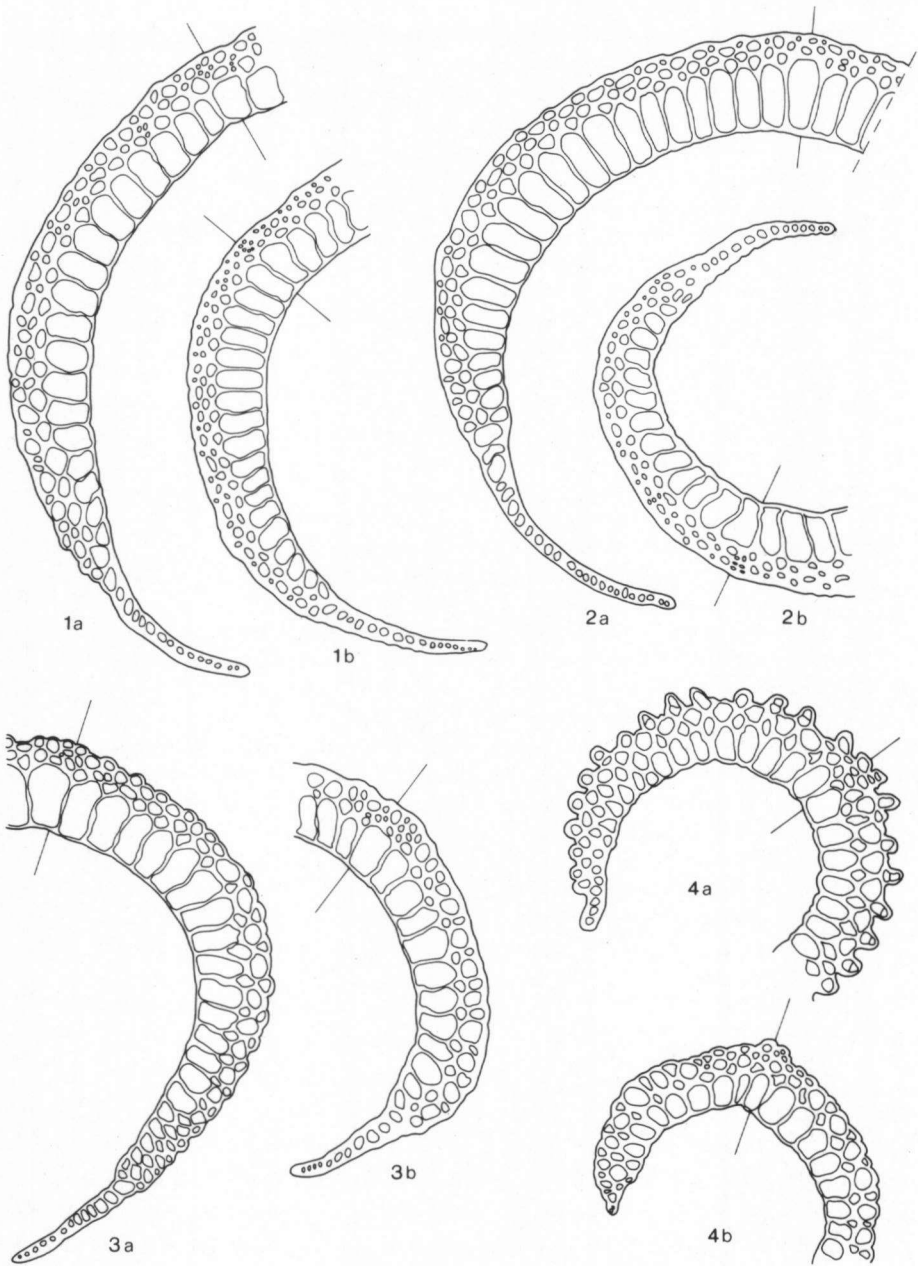
#### Collection nrs. and habitat data:

- Fl. 4014 BOYACÁ: Sierra Nevada del Cocuy; Alto Valle Lagunillas. Boggy valley floor near pool. Predominancy of *Muhlenbergia* sp. (Gram.). Very wet. Alt. 3950 m.
- Fl. 4034 BOYACÁ: idem as 4014. Associated with *Muhlenbergia* sp., *Ranunculus limoselloides*, *Breutelia chrysea*, *Leptodontium wallisii*, *Thuidium delicatulum* and *Anastrophyllum* sp. Very wet. Alt. 3950 m.
- Fl. 3901 CUNDINAMARCA: Páramo in the headwaters of Río Chuza between Páramo de Palacio and P. de Chingaza. *Sphagnum* bog with *Sphagnum sancto-josephense*, *Rhacocarpaceae purpurascens* and *Oreobolus* sp. (Cyp.). Alt. 3700 m.
- Fl. 3922 CUNDINAMARCA: idem as 3901. In bog, associated with *Breutelia tomentosa* and Cyanophyta. Alt. 3750 m.
- Fl. 3920 CUNDINAMARCA: idem as 3901. In bog, associated with *Disterigma empetrifolium* (Eric.) and *Breutelia subarcuata* (sensu Robinson, 1967). Alt. 3750 m.

- Fl. 4289 CALDAS: Nevado del Ruiz (road Manizales – Refugio); border superpáramo – grasspáramo. On decayed *Distichia muscoides* cushions on damp soil along streamlet, associated with *Chorisodontium speciosum*, *Herbertus subdentatus* and *Anastrophyllum leucostomum*. Alt. 4200 m.
- Fl. 4285 CALDAS: idem as 4289. Moss cushion on sloping ground, together with *Chorisodontium speciosum*. Alt. 4200 m.
- Fl. 4263 CALDAS: Nevado del Ruiz (road Manizales – Refugio); lower superpáramo with *Distichia muscoides*-*Plantago rigida* cushion bog. On mineral soil with superficial draining, between vascular cushions. Alt. 4250 m.
- Fl. 4269 CALDAS: idem as 4263. Associated with *Calamagrostis ligulata* (Gram.), *Oritrophium limnophyllum* ssp. *mutisianum* (Comp.) and *Scirpus* sp., sect. *Isolepis* (Cyp.). Alt. 4250 m.
- Fl. 4260 CALDAS: idem as 4263. On mineral soil on top of vascular cushions, between *Festuca* sp. (Gram.) and *Disterigma empetrifolium* (Eric.). Alt. 4250 m.
- Fl. 4261 CALDAS: idem as 4263. Idem as 4260. Alt. 4250 m.
- Fl. 4262 CALDAS: idem as 4263. On decaying *Distichia muscoides* cushion together with *Disterigma empetrifolium* (Eric.), *Pernettya prostrata* (Eric.), *Campylopus tunariensis* and *Cladonia* sp. (Lich.), Alt. 4250 m.
- Fl. 4266 CALDAS: idem as 4263. Terrestrial. On soil, associated with *Polytrichum juniperinum*. Alt. 4250 m.
- Fl. 4359 CALDAS: Nevado del Ruiz; Termales. High Andean *Weinmannia* timberline forest. On roadside rocks together with *Campylopus pittieri*, *Plagiochila* sp. and *Scapania portoricensis*. Atmospherically humid. Alt. 3250 m.
- Fl. 4363 CALDAS: idem as 4359. On rocks together with *Prionodon luteo-virens*, *Anastrophyllum leucostomum* and *Leptoscyphus cleefii*. Atmospherically humid. Alt. 3250 m.
- Fl. 4120 ARAUCA: Sierra Nevada del Cocuy; Alto Patio Bolos. Lower superpáramo. Dense moss cushions on mineral soil between rocks. Atmospherically humid. Alt. 4350 m.
- Fl. 4243 CALDAS: Nevado del Ruiz; lower superpáramo. On volcanic soil between rocks with *Loricaria colombiana* (Comp.). Dense cushions with *Leptodontium pungens*, *Bartramia potosica* and *Mielichhoferia* sp. Alt. 4300 m.
- Fl. 4254 CALDAS: idem as 4243. Dense cushions with *Rhacomitrium crispulum*, *Anastrophyllum leucostomum*, *Leprocaulon* sp. (Lich.) and *Oropogon loxensis* (Lich.). Alt. 4300 m.
- Fl. 3987 BOYACÁ: Sierra Nevada del Cocuy; Alto Valle Lagunillas. Dense compact cushions on decaying *Espeletia lopezii*-stems, and terrestrial. Associated with *Pernettya prostrata* (Eric.), *Leptodontium flexifolium*, *Bryum billardieri* and *Polytrichum juniperinum*. Alt. 3950 m.
- Fl. 4058 BOYACÁ: Sierra Nevada del Cocuy; Bocatoma valley, border grasspáramo-superpáramo. Epilitic. Alt. 4200 m.

#### RESULTS AND CONCLUSIONS

The observations of costal anatomy in field material showed a striking correlation between substrate humidity and degree of cell wall thickness (table 1). Plants of humid substrates appear to have distinctly thickened costal cell walls (with or without pseudostereids) whereas on dry substrates costal cell walls are usually thin or only slightly thickened (pseudostereids absent). Two specimens however from dry substrates (*Florschütz 4120, 4363*) have thickened cell walls. Since both specimens are from habitats with high atmospheric humidity (the other dry-substrate specimens being collected at sites with low atmospheric humidity, except *Florschütz 4359*) it might be assumed that atmospheric humidity, in addition to substrate humidity, may influence the degree of cell wall thickness, especially on the drier substrates.



Leaf cross sections of (a) field specimens and (b) cultivated specimens. Magnification 450 $\times$  in all figures except 2a (340 $\times$ ).

Figs. 1 and 2: *C. leucognodes-subconcolor* complex (Fl. 4289 and Fl. 4285).

Figs. 3 and 4: *C. pittieri*; lower leaf portion (Fl. 4360) and upper leaf portion (Fl. 3921).

Table 1. Costal anatomy in field specimens and cultivated specimens of the *C. leucognodes-subconcolor* complex as compared with substrate- and atmospherical humidity at the collecting sites. ++ costal cell walls strongly thickened; + costal cell walls thickened; – costal cell walls thin; WW very wet; W wet; DW humid; D dry.

Substrate humidity (nat. cond.)	Atmosph. humidity (nat. cond.)	Costal cell walls in		Collection number (leg. Florschütz)
		field material (nat. cond.)	cultivated material	
WW	D	+	+	4014
WW	D	++	++	4034
W	DW	+	++	3901
W	DW	+	+	3922
W	DW	+	±	3920
W	DW	+	++	4289
W	DW	–	+	4285
W	DW	+	++	4263
W	DW	+	++	4269
DW	DW	±	±	4260
DW	DW	±	+	4261
DW	DW	±	+	4262
D	W	–	±	4359
D	W	+	++	4363
D	W	+	±	4120
D	DW	–	+	4266
D	DW	–	+	4243
D	DW	–	+	4254
D	D	–	+	3987
D	D	–	–	4058

Comparing costal sections in the field material with those in cultivated specimens, a marked tendency is observed for the cell walls to become thicker in culture.

Of ten thick-walled field specimens six specimens became even more thick-walled in culture (4034, 3901, 4289, 4263, 4269, 4363; fig. 1b), two specimens remained unchanged (4014, 3922) and two other specimens (3920, 4120) became rather heterogeneous, yielding thin-walled and thick-walled sections on the same plant.

Of seven thin-walled field specimens, five produced thickened cell walls in culture (4285, 4266, 4243, 4254, 3987; fig. 2b), one became heterogeneous (4359), whereas one specimen remained unchanged (4058).

In view of the apparent importance of habitat humidity as a factor influencing the degree of costal cell wall thickening under natural conditions, it might be assumed that the increasing thickening of the cell walls in the cultivated specimens was caused by the constantly high humidity in the glassboxes. Further studies are necessary to test this assumption.

From our experiments we conclude that the degree of costal cell wall thickness and the presence or absence of (pseudo)-steroids in the *Campylopus leucognodes-subconcolor* complex is environmentally controlled rather than

genetically fixed and therefore cannot be treated as a taxonomic character in this group.

#### DISCUSSION

In addition to the supposed differences in costal anatomy, *C. leucognodes* and *C. subconcolor* are sometimes distinguished by a difference in laminal cell shape (cf. Frahm, 1978). While in *C. leucognodes* laminal cells are oval-elongate (Thériot, 1939: "hexagonales-allongées"; Robinson, 1967: "very elongate"), those of *C. subconcolor* are rectangular. A study of the type specimen confirmed these observations, although in the type of *C. leucognodes* we found leaves with rectangular cells mixed with oval-elongated cells. In additional material of this complex investigated by us, we have been totally unable to draw a line between the two species using laminal cell shape as a characteristic. In fact, all intermediates were found. Frahm (1978) also noted differences in the leaf tip (longer in *C. leucognodes*) and the nervebase (narrowed in *C. subconcolor*), but our observations of types and of additional material do not confirm Frahm's findings. Consequently we have to conclude that *C. leucognodes* and *C. subconcolor* are to be treated as synonyms. Another synonym is *C. argyrocaulon* (C. Müll.) Broth. (see Florschütz, 1975 and Frahm, 1978).

The following synonymy results:

*C. subconcolor* (Hampe) Mitt. – *Dicranum*; Linnaea 32: 138. 1863.

*C. argyrocaulon* (C. Müll.) Mitt. – *Dicranum*; Linnaea 38: 588. 1874.

*C. leucognodes* (C. Müll.) Par. – *Dicranum*; Nuov. Giorn. Bot. Ital. n. ser. 4: 32. 1897.

## II. *Campylopus pittieri* Williams

#### INTRODUCTION

Williams (1908) described *Campylopus pittieri* as a new species based on Pittier's moss collections from Colombia (type: *Pittier 1088*, NY). The presence of a sporophyte with a strongly curved seta leaves no doubt that the species belongs in *Campylopus*. Robinson (1967) considered *C. pittieri* to be a synonym of *C. argyrocaulon* (C. Müll.) Broth., but Florschütz and Florschütz-de Waard (1975) showed that the costal anatomy of the two species is different and pointed out that *C. argyrocaulon* belongs in the *C. leucognodes-subconcolor* complex. They agreed with Robinson (l.c.) that *Paraleucobryum densifolium* Thér., described by Thériot (1939) on the basis of sterile Colombian material, is a synonym of *C. pittieri*. The costal anatomy of *C. pittieri*, illustrated and described by Florschütz and Florschütz-de Waard (l.c.), is typically "leucobryoid" (two layers of large leucocysts enclosing one layer of small chlorocysts) near the leafbase, whereas near the leaf apex two layers of chlorocysts are present. The cross-section of the upper leaf portion is diagnostic for the species. On the dorsal side of the costa one leucocyst alternates with two chlorocysts (fig. 4a): the "2-1 pattern" as contrary to the "2-2 pattern" in the

*C. leucognodes-subconcolor* complex. The outer chlorocyst projects outwards and produces a longitudinal ridge, which is visible in surface view as a dark line.

Considerable variation of costal anatomy characters of *C. pittieri* was observed in recent Colombian material of this species collected by P.A. Florschütz in 1972 (COL, U). While in some specimens the dorsal ridges were very weakly developed, in others the 2-1 pattern was replaced in the middle of the section by a 2-2 pattern (Fl 4360; fig. 3a). In order to test the stability of this variation, ten specimens of *C. pittieri* were cultivated in a growth chamber under the same conditions as described above for the *C. leucognodes-subconcolor* complex.

#### MATERIAL

Collection nrs. of cultivated specimens:

leg. P.A. FLORSCHÜTZ

3919 CUNDINAMARCA: Chuza; Lag. Seca. Alt. 3700 m. Epilitic.

3921 idem. Terrestrial.

3939 idem. Epilitic.

4036 BOYACÁ: Sierra Nevada del Cocuy; Alto Valle Lagunillas. Alt. 3950 m. Terrestrial.

4038 idem.

4360 CALDAS: Nevado del Ruiz; Termales. Alt. 3250 m. Epilitic.

leg. T. v.d. HAMMEN & R. JARAMILLO

2907 CUNDINAMARCA: Páramo de Palacio. Alt. 3600 m.

3103 CUNDINAMARCA: Páramo de Cruz Verde; Alto de la Viga. Alt. 3450 m.

leg. Mrs. R.A.J. GRABANDT

26/5 CUNDINAMARCA: roadside near Chisacá. Alt. 3700 m.

9/7 CUNDINAMARCA: Páramo de Cruz Verde. Alt. 2790 m.

#### RESULTS

1. After two years of cultivation the cell pattern in the costa remained unchanged in "normal" as well as in deviating specimens, which have a "2-2" instead of a "2-1" pattern in the centre of the leaf section (Florschütz 4036, 4038, 4360; figs. 3a and b).
2. Wall thickness of the costal cells does not change, except at the leaf apex where a slight increase of wall thickness is sometimes observed (Florschütz 4036, 4360, v.d. Hammen 3103).
3. In all specimens there is a tendency for the apical ridges on the dorsal surface of the costa to disappear (figs. 4a and b). While in some specimens they became weak (Florschütz 3921, 4038; v.d. Hammen 3103; Grabandt 9/7), in others they disappeared entirely (Florschütz 3939, 4036, 4360; Grabandt 26/5).

#### CONCLUSIONS AND DISCUSSION

The experiment shows that variation in the costal cell pattern in *C. pittieri* is stable and is not affected by cultivating specimens under identical growth conditions.

The development of apical costal ridges however, is apparently influenced by the environment and should be considered less reliable for species recognition.

The disappearance of the ridges in cultivated specimens is possibly caused to some extent by the increased thickening of the apical costal cell walls, obscuring the outlines of the ridges.

Following Thériot (1939), two varieties can be recognized in *C. pittieri* (Florschütz and Florschütz-de Waard, 1979):

Var. *congestum* (Thér.) Florschütz-de Waard (= *Paraleucobryum densifolium* Thér. var. *congestum* Thér.).

Var. *latilimbatum* (Thér.) Florschütz-de Waard (= *Paraleucobryum densifolium* Thér. var. *latilimbatum* Thér.).

Var. *congestum* was characterized by its relatively long leaves: "feuilles plus longues" (Thériot l.c.: p. 66). The type specimen (Troll 2093, Colombia, PC) appears to stand out particularly by its rather wide and short leaf apex with distinct ridges. Var. *latilimbatum* (type: Troll 2148, Colombia, PC) has a much longer and narrower leaf apex (Thériot: "acumen des feuilles deux fois plus étroit") whereas the ridges are lacking or at the ultimate leaftip faintly visible in cross section. Both varieties have the typical costal cell pattern of *C. pittieri*.

*C. pittieri* var. *latilimbatum* is not very much different in habit from specimens of the *C. leucognodes-subconcolor* complex. The two taxa can be distinguished only by their different costal cell pattern, but deviating specimens of *C. pittieri* with a 2-2 instead of a 2-1 pattern in the centre of the costa may be difficult to identify with confidence. The occurrence of such specimens shows that the two species are indeed very closely related.

Apparently the two varieties represent extreme phases of the variation in *C. pittieri*. The experiments have shown that some of this variation (e.g. the development of costal ridges) is environmentally controlled. The extent of genetically controlled variation in this species should be the subject of further investigations.

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