The genus Chorisodontium (Dicranaceae, Musci) in the Neotropics.

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Abstract: All the species of Chorisodontium recorded from the neotropical mountains (Bolivia - Costa Rica) have been critically revised. Three species, C. nigricans Herz, C. mittenii (C. Müll.) Broth. and C. wallisii (C. Müll.) Broth. are accepted. Chorisodontium speciosum (Hook. f. & Wils.) Broth. is placed as a variety to C. wallisii.

Resumén: Todas las especies de Chorisodontium conocidas de las montañas del neotrópico (Bolivia - Costa Rica) se ha revisado criticamente. Tres especies, C. nigricans Herz., C. mittenii (C. Müll.) Broth. y C. wallisii (C. Müll.) Broth., son distinguida.

Zusammenfassung: Alle Chorisodontium-Arten der neotropischen Gebirge (Bolivien - Costa Rica) wurden einer kritischen Revision unterzogen. Danach werden drei Arten, C. nigricans Herz., C. mittenii (C. Müll.) Broth. und C. wallisii (C. Müll.) Broth. unterschieden..

INTRODUCTION

Knowledge of the species of Chorisodontium is rather limited up till now. However, a large number of new collections became available in the course of phytosociological studies conducted in the Eastern Cordillera of the Colombian Andes by T. van der Hammen (Amsterdam), P. Jaramillo Mejía (Bogotá) and their collaborators, mainly in the forest belts, by the late P.A. Florschütz (Utrecht) and by A.M. Cleef (Amsterdam) and co-workers, mainly in the páramo belt.

Recently in the framework of the ECOANDES-project more collections of Chorisodontium have been gathered by T. van der Hammen, O. Rangel Churio (Bogotá), J. Wolf and G. van Reenen (Utrecht).

The present study is based on about 100 collections of which complete sets are stored in COL and U. Nearly complete sets are present in FLAS. Type material as well as additional specimens was borrowed from BM, F, H, H-BR, NY, S and US, which help is gratefully acknowledged here. In addition to

herbarium studies, field studies on problems of the variability of species of *Chorisodontium* have been carried out in Ecuador in 1988.

DISTRIBUTION AND ECOLOGY

The genus Chorisodontium is characteristic of the higher elevations of the humid tropical Andes and the subantarctic mires of southern South America. Its important ecological role has been discussed previously, but the taxonomy of this genus has not been treated in detail. Only a key and illustrations were provided by FRAHM (1981). Of the 19 species of Chorisodontium listed in the Index Muscorum (WIJK et al. 1959), 14 were accepted in this publication. Of these species, one is endemic to the Ile d'Amsterdam in the Indian Ocean. Eight species are confined to Patagonia and subantarctic islands, one of them also found recently in New Zealand (BARTLETT & FRAHM 1983). Chorisodontium burrowsii Allis., described from New Zealand, belongs to another genus (BARTLETT & FRAHM 1983). Another species, Chorisodontium falcatum, described by MAGILL (1981) from South Africa, is regarded as synonymous with *Platyneurum laticostatum* (Card.) Broth. Although related to *Chorisodontium*, the monotypic *Platyneurum* differs by the absence of stereids in the transverse section of the costa and a coarsely papillose back of the costa. In the Andes between Bolivia and Costa Rica five species have been recorded by Frahm (1981).

The subantarctic species of Chorisodontium occur in bogs. Similarly C. nigricans from Bolivia and Peru grows on wet rocks in the alpine belt of the Andes. Only C. mittenii from the northern Andes is epiphytic in subalpine forests. Thus on account of its absence from other subantarctic regions such as New Zealand, Tasmania and South Africa it can be assumed that this genus originated in Southern South America, perhaps after the split of the Gondwana continent. After the raising of the Andes in the Teriary this genus successfully invaded the Andes like many other genera where one taxon (presumably the youngest in evolution) adapted to epiphytism.

MORPHOLOGY

Chorisodontium species resemble in general appearence large species of Campylopus and in many anatomical details species of Dicranum. Accordingly all species have originally been described as species of Dicranum. They can be distinguished actually only by the long excurrent, awnlike costa, which fills the leaf tip and is somewhat widened at the end of the lamina, where the lamina is bistratose and cannot be distinctly separated from the costa. The areolation with often thick and pitted cell walls, the alar cells and also the transverse section of the costa with a median row of enlarged (deuter) cells and several rows of ventral and dorsal stereids are similar to those of certain species of Dicranum. The costa is narrow but enlarged just above the leaf insertion so that the alar cells seem not to reach the costa.

Within the genus two morphological groups corresponding to the ecological differences and the two distribution patterns can be

recognized. The subantarctic species (including C. nigricans from Bolivia) are characterized by shorter leaves ranging from 3 to 8 mm in length (9-11 in C. fulvastrum endemic to Ile d'Amsterdam), by smooth leaf tips, lax areolation with less thickened cell walls, lacking or less developed alar cells and a different spore size (18-20 µm). The northern andine species has leaves 11-15 mm long, incrassate and pitted lamina cells, conspicuous alar cells and larger, often multicellular spores ranging from 20 to 80 µm. The size of the spores cannot be indicated exactly since they germinate precociously in the capsules, developing 2-4 cell stages with chlorocysts (fig. 1). As shown by measurements of about 100 spores of one capsule of Chorisodontium mittenii, three different classes of spore sizes can be recognized (fig. 2): brown, unicellular spores ranging from 20-25 µm which seems to be the basic spore size of this species, green, unicellular spores ranging from 35-55 µm (enlarged spores in the stage of development), and green multi(2-4)cellular spores which are germinated. All these characters can be interpreted as special adaptations to epiphytic growth: alar cells for water uptake, incrassate cell walls as protection against desiccation and shrinking and large spores which divide in the capsule to facilitate germination in cushions of other bryophytes on nearby branches and stems.

The distinguishing characters between all northern andine species as given by Frahm (1981) concern serration of leaf tips, length of the capsule or length of the excurrent part of the costa and are relatively insignificant and make the identification of certain specimens difficult. The differentiation of the four northern andine species Chorisodontium mittenii (C. Müll.) Mitt. (including C. germainii (C. Müll.) Broth. and C. spectabile (Schimp. ex Britt.) Broth.), C. setaceum (Bartr.) Bartr., C. speciosum (Hook.f. & Wils.) Broth. and C. wallisii (C. Müll.) Broth. (Frahm 1981) was based mainly on the study of the type material. Field studies in Ecuador and subsequent critical examination of herbarium specimens revealed that these four species cannot be



Fig. 1: Spore of Chorisodontium mittenii (Frahm 260a), four cell stage

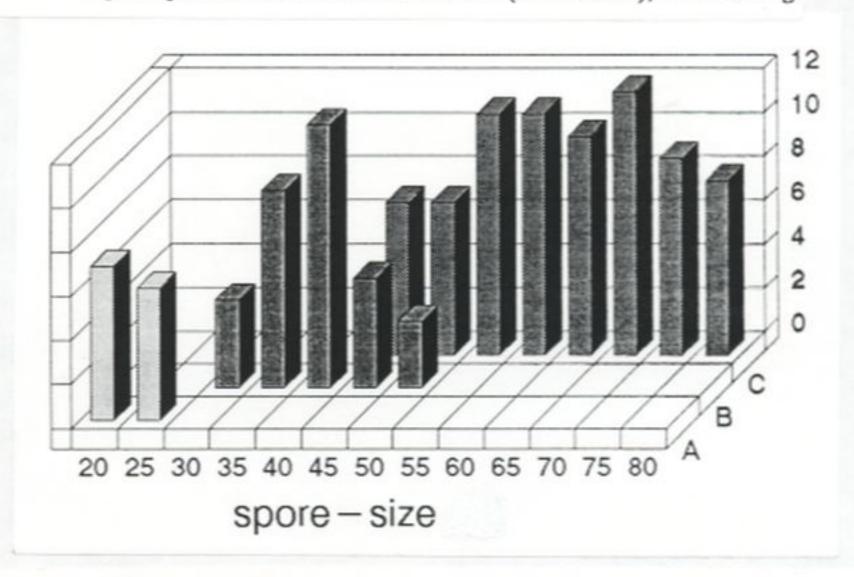


Fig. 2: Variation of spore-size in *Chorisodontium mittenii (Frahm 260a*).

A: brown unicellular spores, B: green unicellular spores, C: green multicellular spores.

distinguished. Chorisodontium setaceum had been described originally as Dicranoloma setaceum and was transferred to Chorisodontium by Bartram (1929): "If not a form of C. speciosum, it is evidently very closely related and should take the name of Chorisodontium setaceum (Bartr.) comb. nov." The distinction of the remaining three species is problematical. In the field and in herbarium material, two extreme forms can be distinguished. The first (fig. 3) is laxly foliate with long patent and often recurved leaves. The leaf apex is 2.5 - 4 times longer than the leaf base. The apex is strongly and spinosely dentate. The upper laminal cells are elongate. This form is represented by the types of C. mittenii, C. spectabile and C. germainii. It is found usually epiphytic in subalpine forests between 3000 and 4000 m elevation, rarely also on soil in comparable low elevation of 3000 m, but conspicously in secondary habitats such as roadside banks. The leaves are falcate at lower elevations but more or less straight to slightly curled at higher elevations. The second extreme expression (fig. 4) is appressed foliate. The leaf apex is short, only 1-1.5 times longer than the leaf base, and smooth or only slightly serrate. The upper laminal cells are oval to elongate-oval. Its appearence resembles much that of Campylopus cavifolius Mitt., which often grows mixed with it. It occurs only on wet soil and over wet rocks in páramos between 3700 and 4000 m. This form is represented by the type of C. wallisii. This morphological differentiation would allow one to distinguish two species, which are also ecologically distinct. However, there is an inter-mediate between both extreme expres-sions. This intermediate shows more or less appressed foliate or erectopatent leaves which have, however, long leaf apices (3 times longer than the leaf base), elongate upper laminal cells but weakly serrate leaf tips. This form is found also on soil in páramos between 3400 and 4000 m elevation and is represented by the type of C. speciosum. It is hardly possible to clarify the natural relationships between these morphological groups based on the study of herbarium material. Principally there seem to be four possibilities: (1)

There is one species with three modifications caused by different habitats and different elevation, (2) there are two species (represented by the extreme forms), and one hybrid in the overlapping part of the altitudinal range, (3) there are three different species, or (4) one species with three different varieties depending how the differentiating characters are valued. In the first case it would not be possible to differentiate between these forms to be recognized, which are also ecologically distinguished, the second case of hybridisation is very hypothetical and can not be confirmed, and distinguishing three taxa seems not to be appropriate because of the presence of an intermediate taxon. Therefore the two extreme expressions are distinguished here on a species level (C. mittenii and C. wallisii) and the intermediate (C. speciosum) is placed as a variety to C. wallisii, because it shares with the latter the habit and the habitat and occurs within the same range. This taxonomic solution seems also to be open for all interpretations.

The shape of the capsule is very variable independently of these gametophytic differences and therefore the length-width ratios given by Frahm (1981) taken from the type specimens are misleading. It varies even in specimens of *C.* mittenii between 1:2.5 and 1:4 (fig. 5).

KEY TO THE NEOTROPICAL SPECIES OF CHORI-SODONTIUM

1 Leaves 8 mm long, loosely appressed to the stem; cell walls less thickened

C. nigricans

1 Leaves 10-15 mm long, spreading; cell walls strongly thickened and pitted

2 Leaves distant, spreading, the excurrent part of the nerve 3-5 times longer than the lamina. Leaf apex sharply or spinosely serrate. Plants usually epiphytic, rarely epigeal

C. mittenii

2 Leaves closely appressed, the excurrent part of the costa 1-2.5 times longer than the lamina. Leaf apex nearly smooth to finely dentate. Plants on wet soil in páramos 3 The excurrent part of the costa as long as the lamina. Upper laminal cells oval

C. wallisii

3 The excurrent part of the costa three times as long as the lamina. Upper laminal cells elongate C. wallisii var. speciosum

1. Chorisodontium mittenii (C. Müll.) Broth., Nat. Pfl. ed. 2,10: 204, 1924. Dicranum mittenii C. Müll., Syn. Musc. 2: 600, 1851. Type: Ecuador, prope Quito, Jameson s. no. (BM, lectotypus nov., isolectotypes FH, NY, fig. 6A, 7D). Chorisodontium germainii (C. Müll.) Broth., Nat. Pfl. ed. 2,10: 204, 1924, syn. nov. Dicranum germainii C. Müll., Nuov. Giorn. Bot. Ital. n. ser. 4: 31, 1897. Type: Bolivia, Germain (lectotype, H-BR, fig. 6D). Chorisodontium spectabile (Schimp. ex Britt.) Broth., Nat. Pfl. ed. 2,10: 204, 1924, syn. nov. Dicranum spectabile Schimp. ex Britt., Bull. Torrey Bot. Club 13: 475, 1896. Type: Bolivia, pr. Sorata, Mandon 1609 (isotype, PC, fig. 7B).

Chorisodontium splendens (Hook.f. & Wils.) Broth. ex Crum, Svensk Bot. Tidskr. 51: 199, 1957.

Dicranum goudotii Hampe, Ann. Sc. Nat. Bot. ser. 5,3: 365, 1865, syn. nov. Type: Colombia, Bogotá, Tolima "ad truncos inf. nivem", Goudot 34 (holotype, BM). (fig. 3)

Plants to 6 cm high, equally foliate, yellowish brown. Leaves to 18 mm long, erect spreading when dry, the upper ones longer and somewhat flexuose, often falcate, from broad ovate base longly acuminate. Costa longly excurrent in a coarsely serrate awn, the excurrent part of the costa 3-5 times longer than the lamina, in transverse section with a median row of enlarged cells and ventral and dorsal bands of stereids, smooth at back. Alar cells large, brownish, numerous, thick walled, reaching the costa. Basal lamina cells with conspicuous thickened and pitted cell walls, ca. 100-125 x 7-10 µm; upper lamina cells shorter and narrower,

ca. 60-80 x 5-7 µm.

Seta yellowish or light brown, about 2 cm long, erect. Capsule 2-3 mm long, erect, cylindric, dark brown or blackish when old, contracted at the mouth, 2.5-4 times longer than broad. Operculum rostrate, half as long as the urn. Spores 20-80 µm.

Distribution (fig. 8): Costa Rica: Heredia, Las Vueltas area, Crosby 6532, 6529 (MO); Cerro de la Muerte, Schultes 12028 (FLAS). Panama: Chiriqui, N of Boquete, Crosby 4058 (MO). Colombia: Arauca, Sierra Nevada del Cocuy, Cleef 10170. Boyacá, Peña de Arnical, Cleef 9414, 9435; Páramos al NW de Belén, Cleef 2900; Páramo de la Rusia, Cleef 7085; Páramo de Pisva, Cleef 4501, 4726; entre Arcabuco y Villa de Leiva, v.d. Hammen et al. 1637; Páramo de Chita, Cleef 9925; Sierra Nevada del Cocuy, Florschütz 4203, Cleef & Florschütz 5964, Cleef & v.d.Hammen 10342; Vado Hondo, Siberia, Cleef 9362 (U). Caldas, Nevado del Ruíz, Salamanca et al. 24, Cleef & t'Hart 2378 (U). Cauca, Parque Nacional del Puracé, v.d.Hammen & Jaramillo 3594, 3705, 3707, Cleef 2626; camino de Pilimbala al Puracé, v.d.Hammen et Jaramillo 3636 (U). Cundinamarca, Subachoque, Páramo El Tablazo, Frahm 885240, 885238 (COL). Páramo de Sumapaz, Mägdefrau 1382 (hb. Frahm), Cleef & Jaramillo 225, 226, Cleef 201; Páramo de Palacio, Florschütz 3860, Cleef 9586; Páramo de Chisacá, v.d. Hammen & Jaramillo 4292; El Boqueron, Troll 2098 (JE); Camino Páramo de Guantiva-Susa, v.d.Hammen & Jaramillo 1652, 1654; Al Sur de la Laguna La Jequera, v.d.Hammen & Jaramillo 1650, 1606; S of Laguna Jequera, v.d. Hammen & Jaramillo 1642 (U); Sabana de Bogotá, Schultes 12233, 12269 (FLAS). Páramo de Sumapaz, Cleef 764, 763; Cordillera de La Leonora, v.d.Hammen & Jaramillo 3779; Páramo de Chisacá, v.d. Hammen & Jaramillo 4366; Páramo de Guasca, Florschütz 3763, Cleef 410, 415 (U), Schultes 239a (FLAS); Páramo de Cruz Verde, Cleef & Jaramillo 3116, 3137; Cuchilla El Tablazo, Linares & Bulla 328; Quebrada de Aguas Claras, v.Reenen et al. 3130; Cabeceras de la Quebrada Chuza, Cleef 9663. Magdalena, Sierra Nevada de Santa Marta, Rangel et al. 841, v.d.Hammen 4546. Meta, Páramo de Sumapaz, v.Reenen 2700, 2820, Cleef 1219, 8024; Cerro Nevado del Sumapaz, Cleef 7834. Santander, Filo de la Jequera, v.d. Hammen & Jaramillo 1647; Tolima, Nevado del Tolima, v.d. Hammen & Jaramillo 3592 (U). Risaralda, Volcán de Santa Rosa, Wolf 1166, 1186; Sza. Rosa de Cabal, v.Reenen 811, 944 (U). Venezuela: Mérida, Sierra Nevada, Teleférico, Cleef & Huber 4783. Griffin 289, 444, 538, 616, 670, 698, 933, 1288, 8821; Ruiz-Terán 6789, 7036, 7944, 8409, 8486; Earl Bishop s. no. (FLAS). Ecuador: STEERE 1948. Azuay: Area Nacional de Recreacion "Cajas" 2°48S, 79°14W, Lewis 78-2418 (NY). Carchi: road Tulcán -Maldonado km 30, Páramo El Angel, Frahm et al. 232, 260, 260a, 268, 279, (U); ibid. W of Pass, upper montane rainforest, Frahm et al. 182 (U); Peru: HEGEWALD 1975, SCHULTZE-MOTEL & MENZEL 1986. Bolivia:

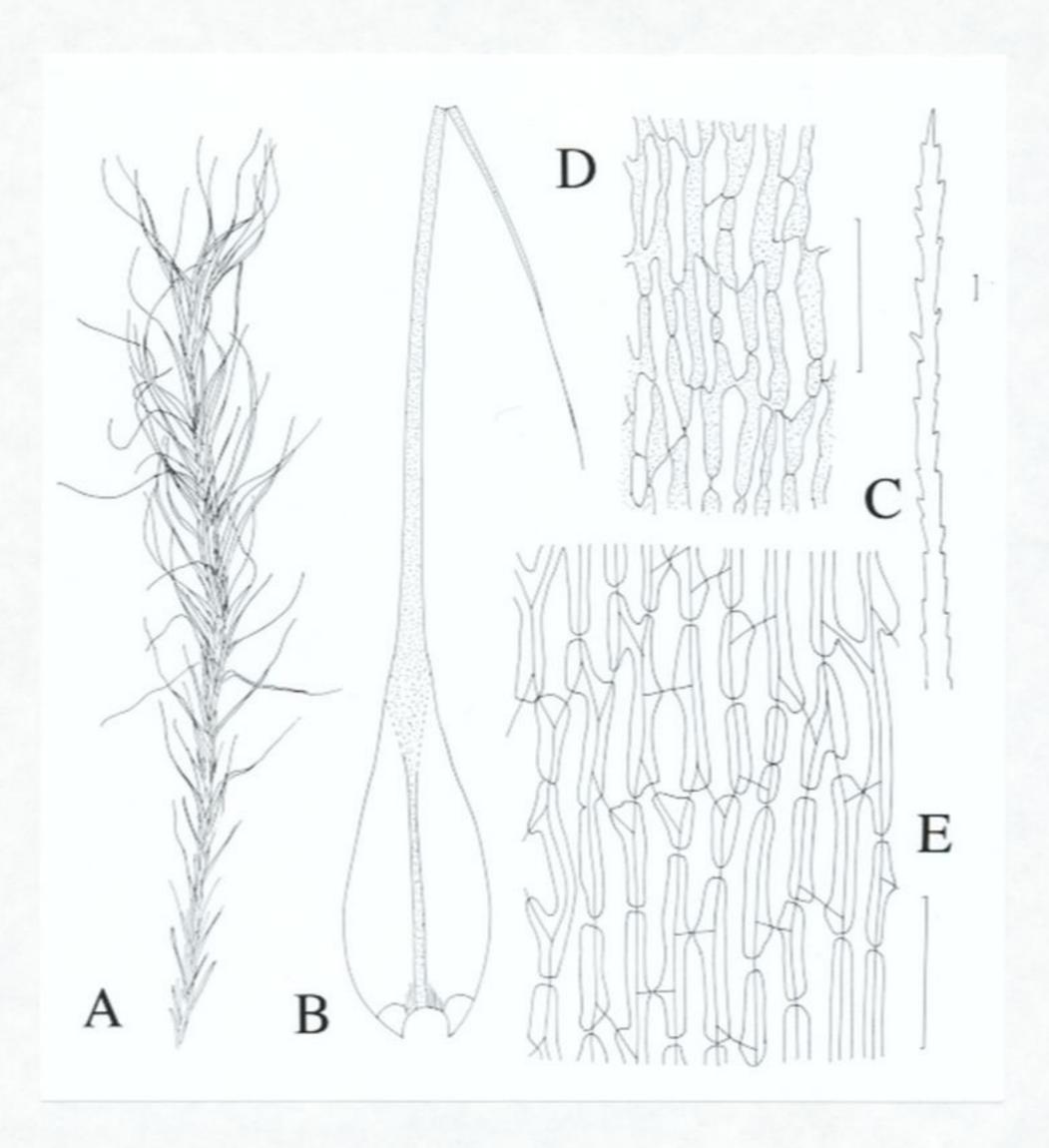


Fig. 3: Chorisodontium mittenii (Frahm 260). A: Plant, nat. size 7 cm; B: Leaf, orig. length 18 mm; C: Leaf tip; D: Upper laminal cells; E: Basal laminal cells. Scale = $50 \, \mu m$

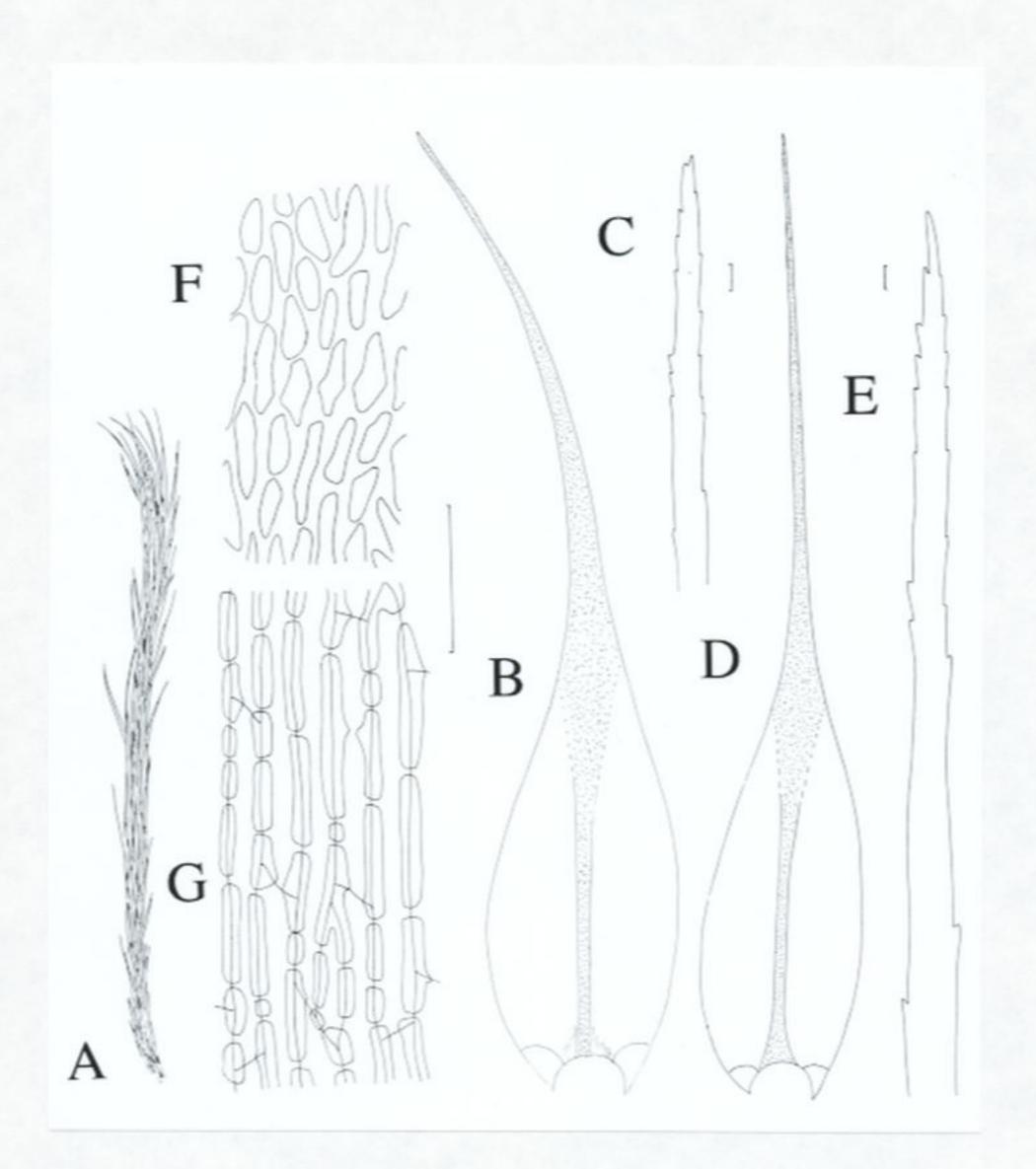


Fig. 4: Chorisodontium wallisii var. wallisii (Frahm 221). A: Plant, nat. size 5 cm;
B: Stem leaf, orig. length 13 mm; C: Leaf tip of B; D: Upper stem leaf, orig.
length 13 mm; E: Leaf tip of D; F: Upper laminal cells; G: Basal laminal cells.
Scale = 50 μm

1975, SCHULTZE-MOTEL & MENZEL 1986. Bolivia: HERMANN 1976; Cochabamba, Siberia, Vogel s. no. (hb. Frahm); W face of Cerro Chua Laguna N of Corani, Lewis 79-2186, 79-2372A, 79-2170 (F). Waldgrenze über Tablas, Herzog 2885 (JE).

Chorisodontium. wallisii (C. Müll.) Broth., Nat. Pfl. ed. 2,10: 204, 1924. Dicranum wallisii C. Müll., Linnaea 38: 590, 1874. Type: Colombia, Prov. Antioquia, Páramo de Ruiz, Wallis s. no. (lectotype, H-

var. wallisii (fig. 4)

BR, fig. 7A).

Plants to 8 cm high, brownish below, yellowish above. Stem equally foliate with erect spreading leaves, the upper leaves usually larger. Leaves to 12 mm long, from an ovate base gradually narrowed into a long subula. Costa excurrent in a smooth or slightly denticulate awn, the excurrent part of about the same length as the lamina. Alar cells in a well defined brownish group, decurrent. Basal lamina cells incrassate, pitted, ca. 80-120 x 10-14 µm. Upper lamina cells conspicuously shorter, oval, incrassate but not or slightly pitted, 45-55 x 7-10 µm.

Seta about 15 mm long, yellowish. Capsule 2 mm long, cylindrical, smooth, brown. Operculum and calyptra not seen.

The morphology and habitat of this taxon resemble most that of the subantarctic species of Chorisodontium. Therefore it might be assumed that this taxon is the oldest representative of this genus in the northern Andes and that the epiphytic Ch. mittenii has been derived from this ancestor.

Distribution (fig. 9): Colombia: Caldas, volcán Puracé, Florschütz 4305. Boyacá: Macizo alto de Belén, Cleef 9802. Cundinamarca, Páramo entre Cogua y San Cayetano, Cleef 6184; Páramo de Palacio, Cleef & Jaramillo 4071, Florschütz 3899. Meta, Páramo de Sumapaz, Cleef 1435, 1475a, 8056, 8136. Venezuela: PURSELL 1973. Ecuador: Carchi, km 34-36 on road Tulcán - Maldonado, Páramo E Angel, Holm-Nielsen et al. 5877 (AAU, QCA); 12 km N of El Angel, Buck 10237 (NY, QCA).

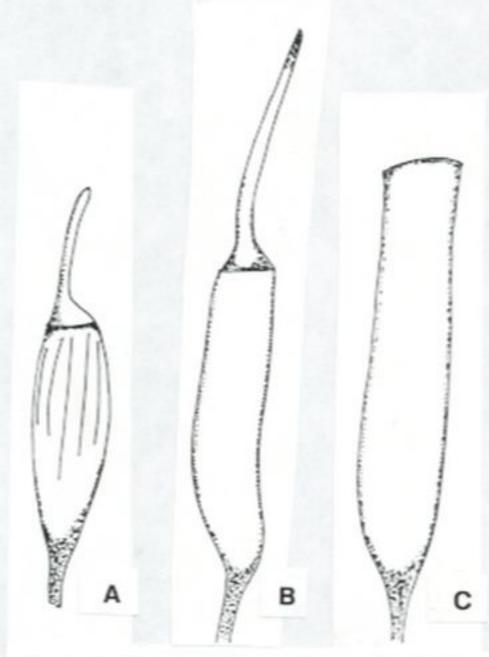


Fig. 5: Variation of shape of capsules of Chorisodontium species. A,B: C. mittenii (A: Frahm et al. 279; B: Frahm et al. 260a); C. wallisii var. speciosum (Frahm et al. 284).

Chorisodontium wallisii (C. Müll.) Broth. var. speciosum (Hook.f. & Wils.) comb. nov. Chorisodontium speciosum (Hook.f. & Wils.) Broth., Nat. Pfl. ed. 2,10: 204, 1924. Dicranum speciosum Hook. f. & Wils., London J. Bot. 6: 291, 1847. Type: Ecuador, Quito, Jameson 134 (holotype, BM, fig. 6C).

? Chorisodontium setaceum (Bartr.) Bartr., J. Wash. Ac. Sc. 19:13, 1929. Dicranoloma setaceum Bartr., Contr. U.S. Nat. Herb. 26: 70, 1928. Type: Costa Rica, Cerro de las Vueltas 3000 m, Standley 43537 (holotype, FH, fig. 6B).

Plants to 10 cm high, in yellowish golden mats. Stems loosely foliate with erect-spreading leaves. Leaves to 14 mm long, from an ovate base narrowed into a long subula. Nerve excurrent in a long smooth awn. Alar cells darker coloured, incrassate, forming a distinct group, decurrent. Basal lamina cells elongate rectangular, incrassate, with strongly pitted cell walls, ca. 140-180 x 10 µm. Upper lamina cells shorter, irregularly pitted, 70-80 x 10 µm.

Seta to 4 cm, straight, brownish. Capsule cylindrical, 4 mm long and 1 mm wide, dark brown, smooth. Operculum obliquely rostrate, 3 mm long.

Distribution (fig. 9): Colombia: Boyacá, Sierra Nevada del Cocuy, Cleef & Florschütz 5964; Monguí, Páramo al Oriente del Pueblo, v.d. Hammen et al. 1659; entre Arcabuco y Villa de Leiva, v.d. Hammen et al. 1637. Caldas, Nevado del Ruíz, Florschütz 4288. Cauca, Páramo de Guanacas, Cleef & Fernandez 669. Cundinamarca, Cordillera de La Leonora 60 km NNE de Bogotá, v.d.Hammen & Jaramillo 3779; Páramo entre Cogua y San Cayetano, Cleef 6451; Páramo de Palacio, Cleef & Uribe 6682, Cleef 311, 4064b, 5249, Cleef & Jaramillo 4047; Páramo de Sumapaz, Cleef 166a, 1130, 1702, 7537, 7645, 8068, 8325, 8339, Cleef & Jaramillo 248, Grabandt & Idrobo 63, 64. Meta, Páramo de Sumapaz, Cleef 1130, 7927. Santander, S of Laguna de Jequera, v.d. Hammen & Jaramillo 1649. Venezuela: Griffin 887 (FLAS). Ecuador: STEERE 1948; Carchi, road Tulcán - Maldonado, Páramo El Angel, 0°48'N, 77°55B W, Frahm et al. 221, 250, 284. Napo, road Quito - Baeza, Laguna de Papallacta, Frahm & Gradstein 400 (U).

Chorisodontium nigricans (Herz.) Broth.,
 Nat. Pfl. ed. 2,10:204, 1924. Dicranum nigricans
 Herz., Beih. Bot. Centralbl. 26(2): 49, 1910.
 Type: Bolivia, "an Felsen bei der Abra de San Benito Prov. Cochabamba 3900 m, leg. Herzog
 1/1908" (holotype, JE; isotype, H-BR, fig. 7C).

Plants to 4 cm high, dark brown below, yellowish at stem tips. Leaves to 8 mm long, from a narrowed base ovate, contracted into a long acumen. Leaf base sheathing, clasping the stem, leaf tips erect-spreading, the upper leaves somewhat homomallous. Costa longly excurrent, in transverse section as in *C. mittenii*. Alar cells differentiated, forming a distinct group of enlarged thick walled cells. Basal lamina cells 80-90 x 5-8 µm with slightly pitted walls; upper lamina cells becoming elongate-oval, 30-50 x 5-10 µm.

Sporophyte not known.

Distribution: Known only from the type locality in Bolivia and Peru (FRAHM 1984).

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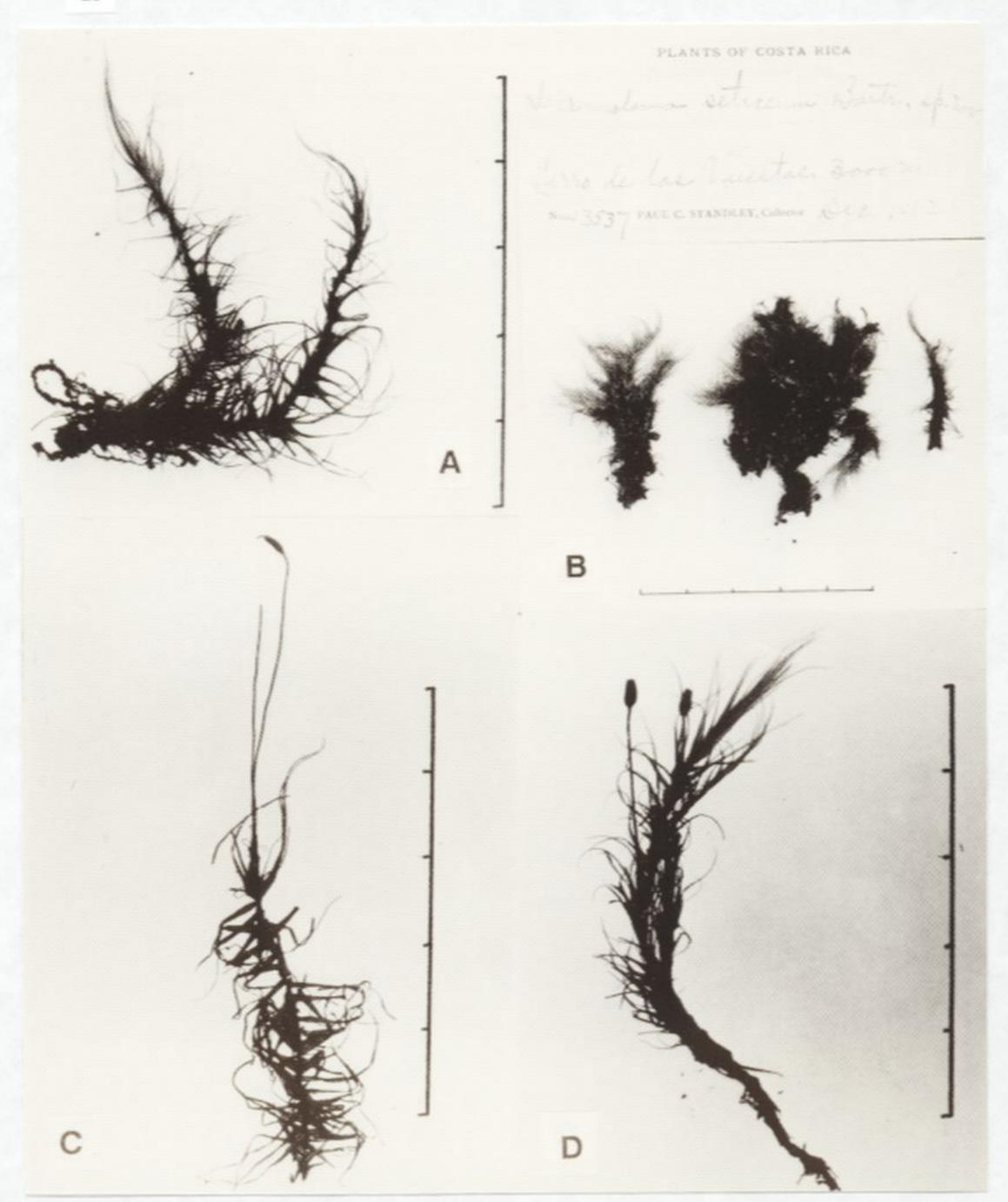


Fig. 6: Type specimens of A: Chorisodontium mittenii (isotype, BM), B: Ch. setaceum (holotype, FH), C: Ch. speciosum (lectotype, BM), D: Ch. germainii (lectotype, H-BR).

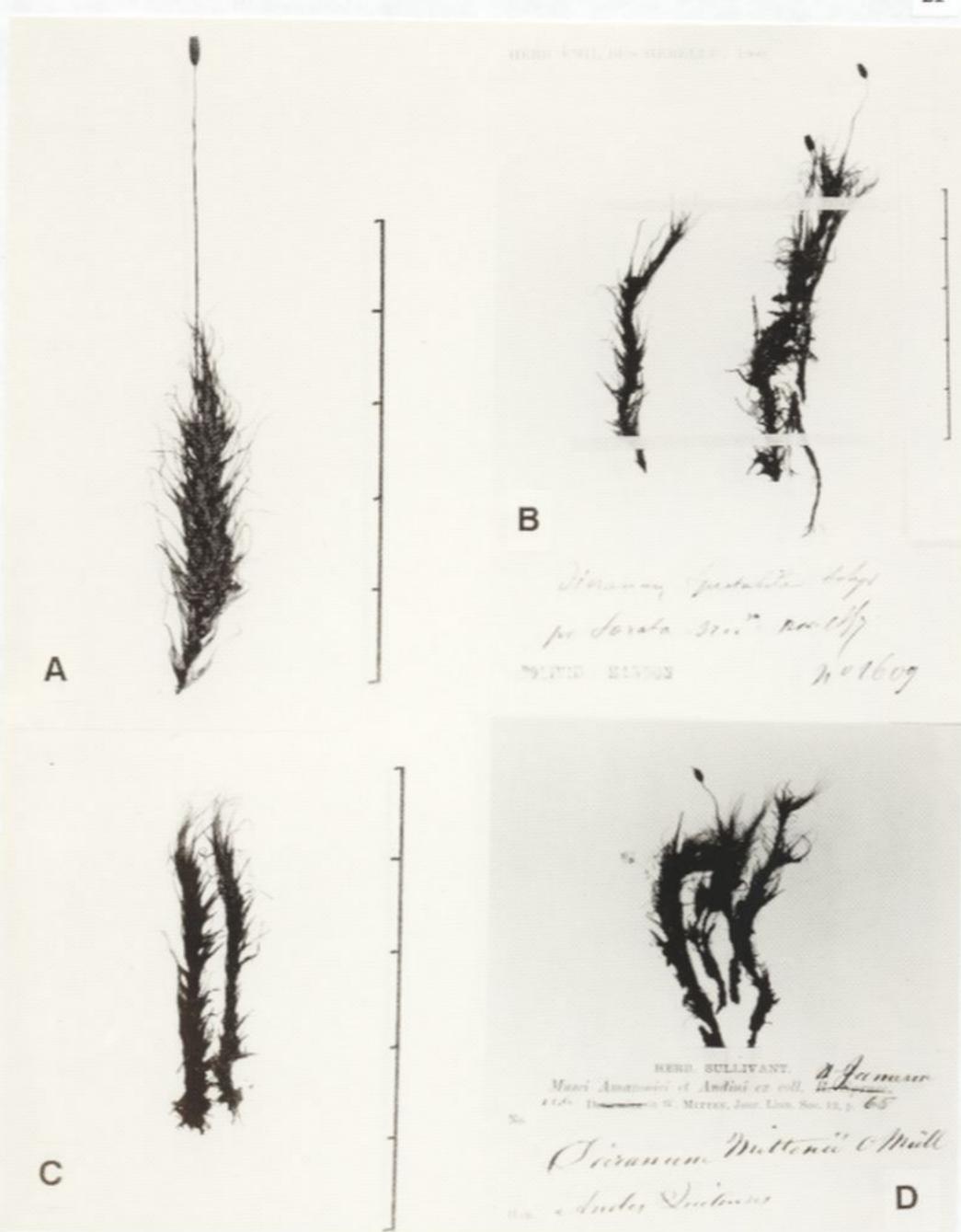


Fig. 7: Type specimens of A: Chorisodontium wallisii (lectotype, H-BR), B: Ch. spectabile (isotype, PC), C: Ch. nigricans (holotype, JE), D: Ch. mittenii (isotype, BM).

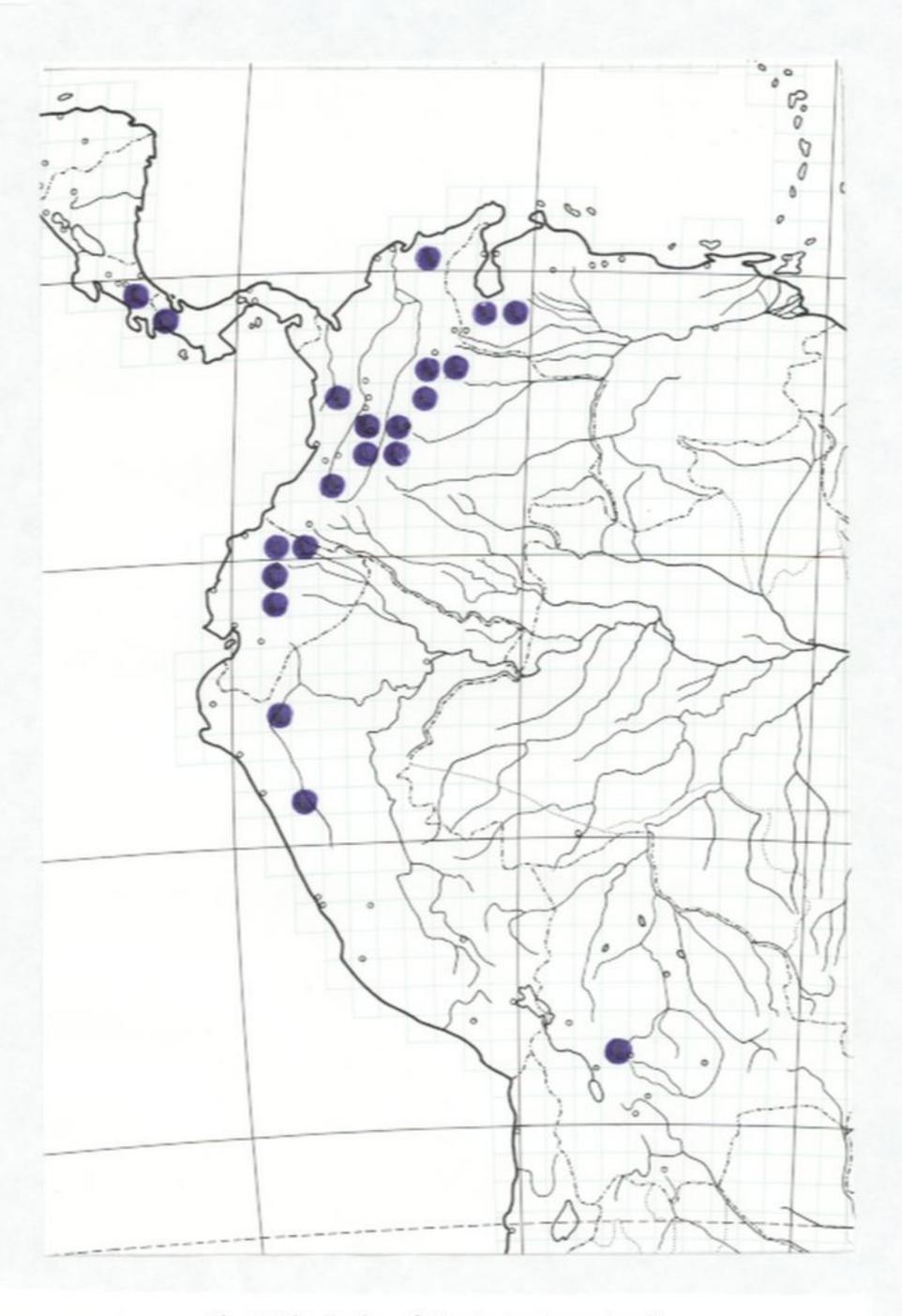


Fig. 8: Distribution of Chorisodontium mittenii.

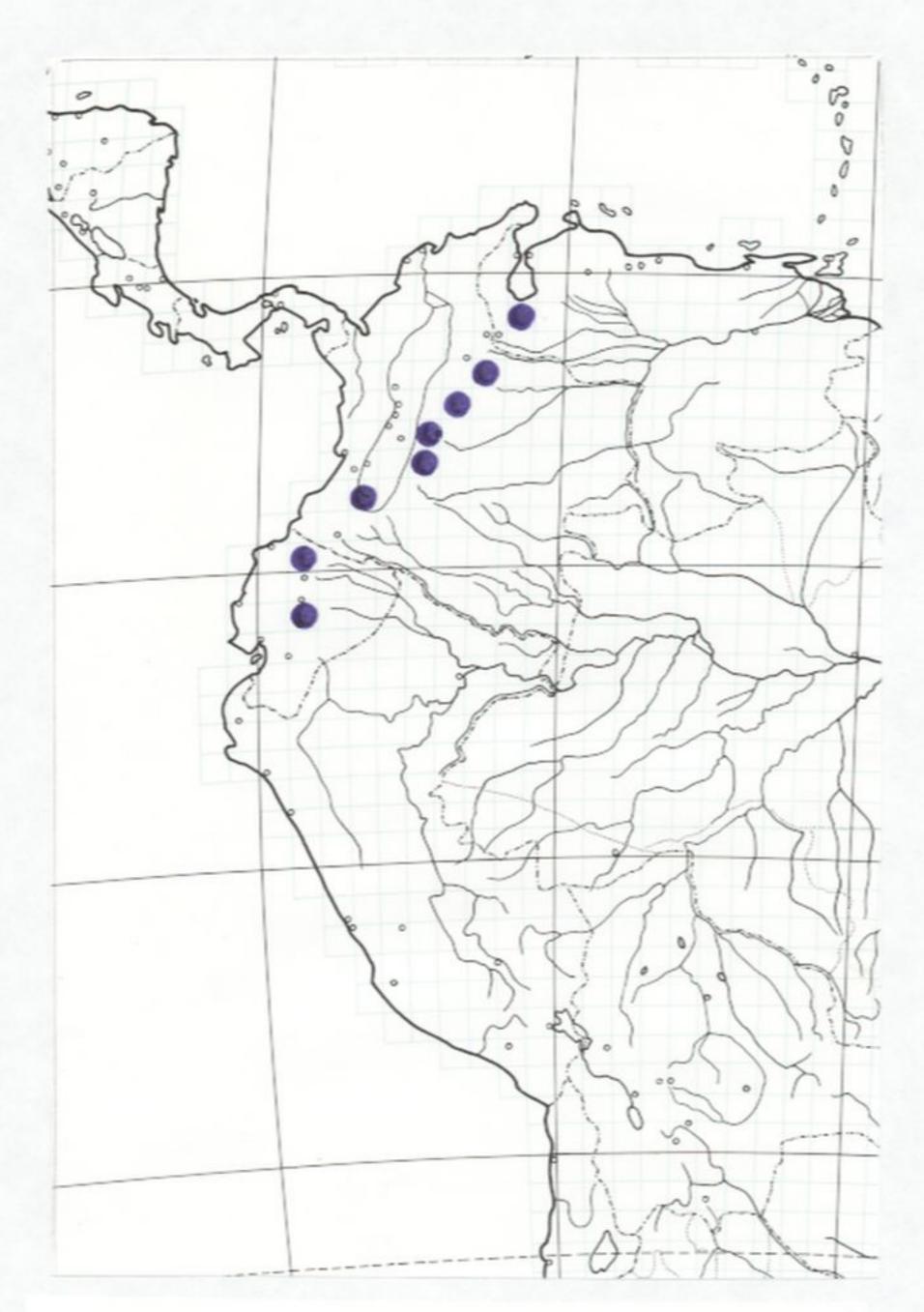


Fig. 9: Distribution of Chorisodontium wallisii.