A contribution to the bryoflora of the Chocó region, Colombia. I. Mosses

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Summary: The Chocó region in Colombia harbours one of the wettest rainforests in the world. Isolated for about 3 million years, it is known for its high rate of endemism in flowering plants, birds and butterflies. Bryologically it is, however, very unsufficiently known. For this reason, a transect was investigated from sea level to 1800 elevation. Ten hectarplots were studied at different altitudes. 125 species of mosses were identified, of which 45 are new records for the departments of Chocó or Risaralda and 17 are new records for Colombia. *Holomitrium aberrans* J.-P. Frahm is described as new. The floristic results allow a first evaluation of the bryogeographical rôle of this region. With 3 endemic species, endemism of mosses in the Chocó region is not as high as in other groups of organisms. Bryologically, the special characteristic of the Chocó mossflora seems to be a meso american floristic element, to which 15% of the species belong. Part of the endemic species of mosses occur also in Panama. It is therefore supposed that the Chocó phytogeographical element is not confined to northern Ecuador and Colombia but continues into the isthmus of Panama.

Based on a calculation of floristic discontinuities, three altitudinal belts could be recognized between sea level and 1800 m, the tropical lowland forest up to 200 m, the tropical submontane forest between 300 and 1500 m and the lower tropical montane forest between 1500 and 1800 m. The delimitation of altitudinal belts agrees quite well with altitudinal studies of tropical rainforest based on bryophytes in other parts of the world.

Several effects could be observed which are probably due to the extreme high humidity: Terrestrial species were found growing on bark or corticolous species on leaves. The cover of epiphytic bryophytes is higher than elsewhere, especially in the lowland forest which shows usually a low bryophyte cover. The percentage of mosses compared with that of hepatics is much lower than elsewhere. Mosses form only about 10% of the bryophyte cover in contrast to 40-50% in the according elevation in other rain forest regions.
The Chocó phytogeographical region encompasses the Pacific coast of Colombia and adjacent Ecuador and extends north to eastern Panama. It is an area of remarkable biological richness and of exceptional phytogeographical interest (Forero 1981, 1985, 1989, Forero & Gentry 1989, Gentry 1978, 1982a, 1982b, 1985, 1986). The region has unusual high endemism of plants, birds, and butterflies, and some authors believe that there are more endemic species in the rain forests of the Chocó than anywhere else in tropical America. The endemism should be due to the isolation of the region since the late Tertiary, following the uplift of the Andean cordilleras. At the plant community level the rain forests of the region are characterized by very high floristic diversity which may exceed that of the richness of the Amazon forests. The unusual biological richness of the area is correlated with very high rainfall which ranges from 3000 mm in northern Ecuador to almost 12,000 mm (!) in the Chocó Department of Colombia. Studies by Drs. Enrique Forero and Ablyn H. Gentry from the Missouri Botanical Garden have provided much valuable information about the flowering plants and ferns of the region. In contrast, mosses and liverworts of the region remain largely unexplored. More than 900 species of mosses have been recorded from Colombia so far. The first checklist of the mosses of Colombia included 750 species (Florschütz-de Waard & Florschütz 1979). Ten years later, the number increased in a second checklist to 877 species (Churchill 1989) and to 895 two years later (Churchill 1991a). In the same year, Churchill (1991b) added another 21 species. Most records are from the montane forests and paramos of the Andes in the interior of the country. In contrast, the lowland rain forests of the pacific coast and the Amazon basin and the adjacent montane forests are considerably less investigated. For the departments of the Chocó phytogeographical region, the following numbers of species of mosses were recorded (Churchill 1989):

<table>
<thead>
<tr>
<th>Department</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chocó</td>
<td>31</td>
</tr>
<tr>
<td>Valle</td>
<td>107</td>
</tr>
<tr>
<td>Cauca</td>
<td>118</td>
</tr>
<tr>
<td>Narino</td>
<td>83</td>
</tr>
</tbody>
</table>

These are comparable low numbers, especially for the department of Chocó. This department has a size of 47205 km² (Forero & Gentry 1989) and is nearly twice as large as Luxembourg, for which 342 species of mosses have been reported (De Zuttere et al. 1985). According to an own evaluation of the literature (Florschütz & Florschütz-de Waard 1979, Churchill 1989, 1991, 1991a), 287 different species of mosses are known so far from these four departments in total.

Although presently accessible only by two roads and consisting still largely of forests, the Chocó Department is considered as "one of the areas most threatened by destruction" (Forero 1989).

The Chocó project

In spite of its high phytogeographical interest, the characteristics of the bryophyte flora of the region remained unknown by lack of bryological exploration. The insufficient knowledge of the bryophytes of the Chocó region is in sharp contrast to the phytogeographical rôle of this region as pointed out by phanerogamists and zoologists. Therefore a preliminary study with representative collections was planned by the author in collaboration with S.R. Gradstein to determine the degree of endemism among the bryophytes of the Chocó, the phytogeographical affinities of the region and the systematic groups of bryophytes involved. The fieldwork has made possible by a grant from the National Geographic Society. Aim of this project was

- to make an inventory of the bryophytes of the Chocó region. To make this inventory as representative and complete as possible in a reasonable time, the transect method was used.

- to make a phytogeographical evaluation of the data with regard to the special phytogeographical rôle of this region as described by phanerogamists and zoologists. This evaluation should clarify whether the high rate of endemism found in other groups of organisms is also found in bryophytes, and if, in which taxonomic groups.
- to make observations on the altitudinal zonation of the region.

- to make observations on the influence of the high humidity on the ecology of bryophytes.

Due to the high humidity of the region, hepatics are predominant and therefore mosses counted only for about 10% of the collections. The results for the mosses are summarized in this contribution, those for the hepatics will be published by S.R. Gradstein in a separate publication.

**Description of localities**

The transect through the Chocó region was studied by S.R. Gradstein and J.-P. Frahm accompanied by Drs. J. Aguirre C. in July and August 1992. It is situated at the western slope of the Western Cordillera (fig. 1) between 400 and 1800 m elevation (fig. 2) and also included the pacific lowland (between 30 and 200 m). The transect mainly followed the two roads connecting the town of Quibdó with the Dept. Risaralda with the exception of the coastal rainforest near Nuquí, which is only accessible by plane and boat, as well as the highest parts of the transect W of Mistrato in the Dept. of Risaralda, which were accessed by mules. Along this transect, ten hectarplots were studied. For every hectarplot a complete inventory of all bryophytes has been made.


2. As 1, mossy lower montane rainforest on ridge, stems densely covered with Lepidozia, Bazzania, Plagiochila, 1600 m elev. 26.7.1992.

3. As 1. Submontane rainforest with Bryopteris, cover of epiphytic bryophytes less than 30%, mainly hepatics, 1200 m elev. 27.7.1992.


8. Dep. de Chocó, Mun. de Nuquí. Amargal at the Pacific coast SW of Arusí, 2 hrs by boat WSW of Nuquí. Lowland rainforest with trees up to 40 m (Ceiba sp.) and buttresses, rich in palms, on hilly surface with small creeks, 30 m elev. 4.-6.8.92.

9. Dep. de Chocó. Road Tutunendo - El Carmen shortly W of point 20. Lightly logged rainforest on ridge with trees up to 25 m and epiphyte cover of 40%, mainly hepatics, 400 m elev. 8.8.92.

10. Dep. de Chocó. Road Tutunendo - El Carmen. 2 hrs footwalk N of point 12. Rather low and wet (logged?) rainforest with trees up to 20 m and epiphyte cover of 60% on slope above small river, 700 m elev. 9.8.1992.

Fig. 1 shows the situation of the study areas, fig. 2 a profile through the transect

**List of collected species:**

* New to the departments of Risaralda (locality numbers 1-5) viz. Chocó (locality numbers 6-10)
** New to Colombia

All collections made by J.-P. Frahm, if not stated otherwise.

Altogether, 358 specimens of mosses were collected. The specimens are deposited in the herbarium of the Instituto de Ciencias Naturales, Universidad Nacional, Bogotá (COL). Duplicates are kept in the herbarium of the University of Utrecht, The Netherlands (U) and the herbarium of the author.

For a phytogeographical evaluation, the distribution patterns are indicated. For the mosses, they are extracted from LATMOSS, a database of neotropical mosses compiled by C. Delgadillo M. The following categories are used:

Cosmopolitan. Pantropical. Included are species disjunct between tropical America and tropical Africa.

Neotropical. Species occurring in Central America, the West Indies, and South America.

Andine. Species ranging to a more or less extend from Colombia to Bolivia.

Extra andine. This category indicates species occurring in Central America, the Carribean and northern South America (meso-american) as well as species confined to South America, northern South America and/or Brazil (south american).

Endemic. Chocó elements occurring along the Pacific coast in Colombia, north to Panama.

The classification of distribution patterns was generalized for some species, of which the
Fig. 2: Profile through the transect studied.
distributional data are obviously incomplete. This may be due to the unsufficient floristic knowledge but also a scattered distribution. For a few species the distributional type could not be determined due to the paucity of records. These species have been omitted from evaluation.

SPHAGNACEAE
Sphagnum meridense (Hampe) C. Müll.
1:9221, on trail bank.- Neotropical.

POLYTRICHACEAE
Pogonatum sp.
3:92436, on trailbank.
Polytrichum juniperinum Hedw.
2:92175, on trailbank. - Cosmopolitan.

BRUCHIACEAE
*Trematodon cf. brevirostris Hampe
3: 92171, single plant on open soil along trail. Known only from Colombia.

FISSIDENTACEAE (det. R. Purcell)
*Fissidens asplenoides Hedw.
5: 92266, on rock. - Pantropical.
*Fissidens cylindrothecus Pursell & Aguirre
6: 92045a, on canopy branch. This species was recently (Pursell & Aguirre 1991) described from a single collection from southwestern Colombia. The type is from Cauca, where it has been collected at 50 m above sea level. Due to this limited range it might be that this species represents a Chocó endemicism. The authors compare it with F. laxus Sull. & Léss., widespread in the Neotropics and Asia, from which it differs mainly by the peristome teeth which are erect when moist and not when dry, which might be interpreted as adaptation to epiphytism. - Endemic.
*Fissidens diplodus Mitt. var. diplodus
7: 92403; 9: 92328, on branch. - Neotropical.
*Fissidens diplodus Mitt. var. mullis (C. Müll.)
Pursell
6: 92401, on small stem.
*Fissidens guianensis Mont. var. guianensis
8: 92328, on rock. - Neotropical.
Fissidens intramarginatus (Hampe) Jaeg.
8: 92273, 92310, along creek. - Neotropical.
*Fissidens mollis Mitt.
On rocks, rarely small stems. - Neotropical.
Fissidens pellucidus Hornsch.
Fissidens weirii Mitt. var. hemicraspedophyllus (Card.) Pursell
1: 92112, 92113. On rocks. - Extra andine.

DICRANACEAE
*Bryohumberia filiformis (Hornsch.) J.-P. Frahm
*Campylopus asperifolius Mitt.
1: 92177; 92147, 92151a, 92159; 92117; 3: 92116.
Typically on canopy branches, rarely on rotten wood. - Andine.
The plants from these collections have conspicuously longer, serrate leaf apices and pitted basal laminar cells compared with specimens from other regions of its range. Since these characters vary even in the collections from the same locality, this effect is attributed to the high humidity of the habitats. Plants from rotten wood are more or less typical, those from canopy branches have much longer leaves. An extreme expression is found in 92157a, which grew in epiphytic tufts of Lepidozia patens.
This species was originally described as species of Dicranodontium, probably because of its very long (unusual for Campylopus) upper laminar cells and the laminar cells not differentiated between basal and upper ones. The sporophyte (found only once in Bolivia) can be attributed to both genera. The transverse section of the costa shows, however, ventral hyalocysts and even no dorsal stereids, a character not found in Dicranodontium. Also the brood leaves produced at stem tips are typical for Campylopus.
**Campylopus cuspidatus (Hornsch.) Mitt. var. cuspidatus
2: 92148 on soil. - Extra andine. A species only known so far from Mexico, Guatemala, Costa Rica, Venezuela and Brazil (Frahm 1991). It has so far not found in the Andes and in so far its occurrence at the western slope of the Andes at 1600 m is remarkable, but is interpreted as an
extension of its Central American range.

*Campylopus huallagensis* Broth. var. weber-baueri (Broth.) J.-P. Frahm 2: 92145 epiphytic. - Andine. So far only known from NE-Peru and a single collection from the Sierra Nevada de Santa Marta in N-Colombia (Frahm 1991).

**Dicroanella sp.**

1: 92210; 3: 92192; 5: 92269; 6: 92431; 8: 92307; 9: 92323, 92430. Always at roadside or trail banks. Due to the lack of a monographic treatment, the specimens remain unidentified.

**Holomitrium aberrans** J.-P. Frahm spec. nov. (Figs. 3, 4)

Planta ad 10 cm altae, virescentes, basi brunnescentes, ramosae, radiculoseae. Folia 9-10 mm longa, bas 0.9 mm lata, patenta, angusti lanceolatae, apicibus tortuosis, marginibus in parte superiore dentatis. Costa 65 μm lata, percurrent, in sezione transversali cellulis stereidibus ventralibus et dorsalis. Cellulae alares distinctae, brunnescentes, cellulae basilares rectangulares, 5-8 μm latae, incrassatae, porosi. Setae ad 2 cm longae, erectae. Theca ad 3 mm longa, erecta, cylindrica, symmetrical, laxis. Dentes peristomi 16, rubres, acuminatae. Spores 12 μm in diam., laeves. Operculum et calyptra ignota.

Plants up to 10 cm high, yellowish, glossy brownish at base. Stems branched, radiculose to the tips. Leaves 9-10 mm long, and 0.9 mm wide at base, patent from stem, narrowly lanceolate, from ovate base contracted into a long acuminate, torulose at tips. Costa narrow, 65 μm wide at base, percurrent, in transverse section with a median band of deuter cells. Leaf margins sharply dentate in the upper half of the leaf. Perichaetial leaves with sheathing base, clasping around the lower 1/4 of the seta. Alar cells brownish, in a distinct, well-defined group. Basal laminar cells longly rectangular, 5-8 μm wide (lumen) and 45-60 μm long, strongly incrassate and pitted, the cell walls as broad as the leaf, becoming shorter towards the leaf tip. Perichaetia 5-10 at stem tips, unisetose. Setae up to 2 cm long, straight, light brown. Urn 3 mm long, erect, symmetric, light brown, smooth. Peristome teeth 16, reddish brown, longly acuminate, simple, strongly papillose at both sides. Spores c. 12 μm in diameter, smooth. Operculum and calyptra not known.

Type: Colombia, Dep. Risaralda. West Side of Cordillera Occidental. Along trail from Jiegudas to Puerto de Oro, W of Mistrato. Lower montane rainforest, canopy ca. 15 m, 1500 m elev. 25.7.1992. Frahm 92151 (holotype MO, isotypes herb. Frahm, COLO); Ibid., mossy lower montane rainforest on ridge, stems densely covered with Lepidozia, Bazzania, Plagiochila, 1600 m elev. 26.7.1992, Frahm 92150, 92155.

The generic placement of this new species is not clear. The specimens resemble a species of *Holomitrium* in the field as well as under the microscope. They have, however, conspicuously long rectangular upper laminal cells, a characteristic typical for the genera Schlepheackea and Eucamptodontopsis. According to B. Allen (in litt.) the specimens incorporate features of all three genera. They have sharply serrate leaf margins as in *Holomitrium* and *Schlepheackea* but not in *Eucamptodontopsis*, long upper laminal cells as in *Schlepheackea* and *Eucamptodontopsis* but not in *Holomitrium*, a habit like *Holomitrium* or *Eucamptodontopsis* but not the pendant habit of *Schlepheackea*. It could thus be a new species of *Holomitrium* with longer upper laminal cells or a new species of *Eucamptodontopsis* with sharply serrate leaves. B. Allen feels that short upper laminal cells are an important characteristic of *Holomitrium*, whereas a species with sharply serrate leaf margins would not be an important change in the generic circumscription of *Eucamptodontopsis*. Therefore he would regard the specimens as new species of *Eucamptodontopsis*. According to the generic description by Brotherus (1924), *Eucamptodontopsis* has ventral deuter in transverse section of the costa, our collections, however, show median deuter cells. The gametophyte of the Chocó specimens resembles much *Schlepheackea* with serrate leaves and linear, pitted laminal cells. The sporophyte is, however, different, having short cysts or setae and an oval urn in *Schlepheackea*, whereas the seta is cylindric on a long straight seta in our plants. The new species is therefore placed provisionally in the genus *Holomitrium*, with which it shares most of the characters but differs by the long upper laminal cells. The name 'aberrans' shall refer to this fact. - Ende-
Endemic.

*Holomitrium flexuosum* Mitt.
2: 92154, epiphytic. - Neotropical.

**Leucoloma cf. mariel** Besch. det. LaFarge
5: 92247, on liana. - So far known from the West Indies and Venezuela.

*Leucoloma procumbens* (Mitt.) Jaeg. det. LaFarge
5: 92241, on liana. - Andine.

**LEUCOBRYACEAE**

*Leucobryum giganteum* C. Müll.
1: 92116; 92206; 2: 92418. On soil and tree trunks.
- Pantropical.

*Leucobryum martianum* (Hornsch.) Hampe

*Octoblepharum albium* Hedw.
8: 92303, on trunk. This widespread species has been collected here in the open around a house and is apparently underrepresented in our collections since it prefers open, exposed habitats and is not to be found in undisturbed forests or the interior of forests. With its stiff recurved leaves it is more xerotolerant and replaced in forest by *O. pulvinatum* with weaker leaves. - Pantropical.
Fig. 4. *Holomitrion aberrans* J.-P. Frahm sp. nov. 1. Leaf, orig. length 10 mm. 2. Leaf apex. 3. Theca, orig. length 3 mm. 4. Basal laminal cells. Scale = 50 μm. Drawn from holotype.
Octoblepharum cocuiense Mitt.
1: 92130, 92208, 92425; 3: 92166; 6: 92424, 92425; 7: 92423; 8: 92281, 92283; 9: 92327; 10: 92348. On tree trunks and buttresses. - An almost pantropical species known from Belize, Costa Rica, Panama, Colombia, Guyana, Peru and Brazil. The distribution is very scattered, although this species is rather conspicuous by its large size and reddish colour and seems therefore not to be overlooked. Found in almost all localities with the exceptions of no. 2, 4 and 5.
Crum (in Magdebrau 1983) published Octoblepharum costatum as new from the surroundings of Quibdó. This species is apparently known only from the type collection. It is described as having a "red tinged thickening resembling a midrib". This is a character frequently found in O. cocuiense. Since the author did not report this apparently very frequent species from the Chocó, it can be assumed that O. costatum could be synonymous with O. cocuiense. The isotype in M was on loan and therefore not available for a revision. Furthermore, Octoblepharum costatum is not accepted in a preliminary list of the accepted neotropical species of this genus by Salazar (1992).
Octoblepharum pulvinatum (Dozy & Molk.) Mitt.
Octoblepharum stramineum Mitt.
6: 92420 on small stem. - Northern South America. This species is (at the present state of knowledge) confined to Colombia, Venezuela, Guayana and the Amazon lowland (Manaus).

CALYMPERACEAE (det. W.D. Reese)
*Calymperes erosum C. Müll. 8: 92306, on trunk. - Neotropical.
**Calymperes nicaraguensis Ren. & Card. 6: 92411, epiphytic. - Central America, West Indies, northern South America.
*Syrrophodon circinatus (Brid.) Mitt.
**Syrrophodon isthmi Reese 6: 92412; 7: 92414. On trunks. This species was described from Panama (Reese 1982) and so far known only from the type locality. It is here reported as new to Colombia and South America. The presently known range (Panama and Chocó) lead to the suggestion that this species belongs to the Chocó phytogeographical element, which extends north to Panama. - Endemic.
Syrrophodon leprieuri Mitt.
1: 92114, 92133; 2: 92145a, 92148; 6: 92417. Epiphytic on stems and on buttress. - Neotropical.
Syrrophodon lycopodioides (Brid.) C.M. 1: 92141, 92160; 2: 92147. Epiphytic on trunks and canopy branches. - Neotropical.
Syrrophodon prolificus Schwaegr. var. tenuifolius (Sull.) Reese 1:92115, 92107. Epiphyllyous (192115) and on rock. - Neotropical.
Syrrophodon rigidus Hook. & Grev. 7: 92413,92434, 92416, on twigs, trunks and lianas. - Neotropical.

POTTIACEAE (det. Ph. Sollman)
*Barbula indica (Hook.) Spreng. 5: 92259; 9: 92400. On roadside and on rock. - Pantropical.
Didymodon laevisatus (Mitt.) Zand. 5: 92265, on bridge. - Andine
*Hyphila involuta (Hook.) Jaeg. 4: 92224; 5: 92263. On concrete of bridge and on rocks along river. Also very frequent on mortar in the town of Quibdó. - Pantropical.
**Pseudosynimpacthis schirruperinae (Par.) Crum 5: 92270, on bridge. - Pantropical.

SPLACHNOBRYACEAE
Splachnobyrum obtusum (Brid.) C. Müll. 6: 92478. Formerly known only from the Caribbean coast of Colombia. - Caribbean.
BRYACEAE
*Bynum limbatum* C. Müll.
4: 92181; 6: 92456, bank of trail and rocks along stream.
*Osculatia columbia* De Not. (Brachymeniophyllum columbiae (De Not.) Broth.)
*Rhodobryum heichianum* (Hornsch.) Par.
*Rhodobryum roseodens* (C. Müll.) Churchill
4: 92178. On soil. Second record of this species endemic to Colombia. Previously known only from Tolima. - Endemic.

MNIACEAE
Plagiomium rynchophorum (Hook.) T.Kop.
1: 92212; 5: 92245. On soil and rocks. - Pantropical.

RHIZOGONIACEAE
Pyrhobryum spiniforme (Hedw.) Mitt.
1: 92139 on soil; 3: 92203 on rotten wood. - Neotropical.
*Rhizogonium lindigii* (Hampe) Mitt.
*Rhizogonium minioides* (Hook.) Wils.
1: 92135 on soil. - Andine, also in Australia and New Zealand.

BARTRAMIACEAE
*Philonotis cf. bernouillii* (C. Müll.) Par.
8: 92305, on soil.
*Philonotis glaucescens* (Hornsch.) Par.
N of Tutunendo 85 mm: 92322.
*Philonotis sp.
6: 92447. On rocks along stream.
*Philonotis sp.
1: 92393, on shaded rock.
*Philonotis uncinata* (Schwaegr.) Brid.

RACOPILACEAE
*Racopilum tomentosum* (Hedw.) Brid.
1: 92108, 92213; 5: 92252. Disjunct between tropical Africa and tropical America.

CRYPHACEAE
*Pseudoxyphacea domingensis* (Spreng.) Buck
(P. flagellifera [Brid.] Britt.)

LEPTODONTACEAE
Leucodontopsis geniculata (Mitt.) Crum & Steere
4: 92229, epiphytic in cocoa plantation. - Neotropical.

PRIONODONTACEAE
Prionodon densus (Hedw.) C. Müll.
5: 92257 epiphytic. - Neotropical.

TRACHYPODACEAE
*Trachypus bicolor* Reinw. & Hornsch. var. viridulus (Mitt.) Zant.
1: 92119 on branch. - Neotropical.

PTEROBRYACEAE
Hildebrandtiella gayanense (Mont.) Buck (Orthostichium g. [Mont.] Broth.) det. Churchill
4: 92235, 92237. On twigs and branches.
Orthostichopsis tetragona (Hedw.) Broth.

METERIACEAE
Meteoropsis Fleisch.
This genus was split by Manuel (1977a, 1977b) into three genera: *Meteoridium, Meteroriopsis* and *Zelometeorium*. *Meteoridium* resembles *Meteoropsis* sect. *Meteoridium* with ciliate calyptrae and spreading leaves. *Meteroriopsis* (resembling *Meteoropsis* sect. *Meteoridium*) as well as the new established genus *Zelometeo*rium have mitrate calyptrae and squarrose leaves. Not regarded the chaotic presentation (Manuel 1977b: Zolometeo, Zerometeo), I am not able to understand the differentiation between *Meteoropsis* ("Leaves squarrose-recurved or spreading with bases clasping") and *Zelometeo* ("Leaves erect to squarrose with clasping or sheathing bases"), especially not on the genus level. In *Zelometeo*, the exostome shall be papillose throughout, in *Meteoropsis* (as in *Meteoridium*), the exostome shall be striolate at base but papillose at tips, a character, which is not much of use since the plants are usually sterile. Therefore the old circumscription of *Meteoropsis* in the sense of Brothe-
Brotherus is retained here with the sections *Meteoriospis* and *Meteoridium* regarded as subgenera.

*Meteoriospis patens* (Hook.) Broth. (Zelometeiron patulum) (Hook. & Mann.)
5: 92249, on leaf; 5: 92250, on twig. - Neotropical.

Papillaria deppei (Hornsch.) Jaeg.
5: 92244, on rocks. - Neotropical.

PHYLLOGONIACEAE
*Phyllogonium viride* Brid.
1: 92121, pendant from twigs. Second record of this species for Colombia. - Neotropical.

NECKERACEAE
*Isoepisum lentum* (Wils.) Britt.

LEUCOMIACEAE
*Leucospermum strumosum* (Hornsch.) Mitt.
6: 92445; 7: 92442, 92443, 92444; 8: 92296. On rotten wood, rarely on trunk. - Neotropical?

DALTONIACEAE
*Hemiaris aurea* (Brid.) Kindb. (Harophyllum aureum [P. Beauv.] Spruce)
1: 92101; 8: 92299. Epiphyllous and on rock. - Panama, Colombia (Antioquia, Magdalena) and Caribbean.

CALLICOSTACEAE
*Callicost a bipinnata* (Schwaegr.) C. Müll.
** Callicost a evansens C. Müll.
6: 92405; 8: 92298 on canopy branches. - Neotropical.

The species of Callicost a are typical for canopy branches. They are rarely found also on twigs in the understory. *Callicost a fendleri* (C. Müll.) Crosby
3: 92199, epiphytic.
** Crossomitrium epiphyllum* (Mitt.) C. Müll.
5: 92243; 6: 92429; 7: 92428, always on leaves and only at low elevations. - Neotropical. *Cyclodictyon albinus* (Hedw.) Kuntze
5: 92251; 8: 92282; 9: 92336; 10: 92368; 92369, Gradstein 8947. On twigs and treelets, also on rotten wood. - Neotropical. *Cyclodictyon lindigianum* (Hampe) Kuntze
7: 92439, on twig. - Colombia (Cundinamarca), Haiti, Cuba. *Cyclodictyon roridum* (Hampe) Kuntze
7: 92440. - Andine (Mexico-Bolivia). *Cyclodictyon turrisetum* (Mitt.) Kuntze
3: 92194; 10: 92357, on trunks and lianas. *Cyclodictyon varians* (Sull.) O. Kuntze
10: 92350, on trunk. - Neotropical. *Cyclodictyon sp.*
3: 92194.
*Hookeriopsis crispa* (C. Müll.) Jaeg.
9: 92330, on rotten wood. - Neotropical. ** Hookeriopsis obsoletinervis Thér.
3: 92201; 5: 92254; 10: 92362, on twigs, base of tree. - Caribbean. *Neobryophylla diversifolia* (Mitt.) Welch & Crum
1: 92133, 92138; 92427, 92207; 2: 92144, 92146, 92153; 9: 92152, epiphytic. - Neotropical. *Lepidodrium scabrosum* (Schwein.) Steere
det. Churchill 8: 92290. 
*Lepidodipilum muelleri* (Hampe) Spruce 10: 92351, 92358. On branch and trunk. - ?
**Lepidodipilum purpurascens** Schimp. ex Besch. 2: Gradstein 8472, 92143. On dead branch and wet rocks. - Carribbean.
*Lepidodipilum stolonaceum* C. Müll. 1: 92124. On rocks in stream.
**Lepidodipilum surinamense** C. Müll. 5: 92258, on twigs. 8: 92300 with Orthostichopsis tetragona det. Churchill. - Neotropical.
*Lepidodipilum tortifolium* Mitt. 8: 92293, on twig.
*Lepidodipilum* sp. 8: 92276, 92272, 92278, on rocks in stream. 5: 92220; 10: 92354, on rocks. 8: 92280; 9: 92339, on rotten wood. - Carribbean.
**Pilotrachidium callicostatum** (C. Müll.) Jaeg. 1: 92132, on trunk. 
**Schizomitririum ciliatum** (Schimp.) Bowers 8: 92313, on rotten wood. - Mexico, Honduras, Costa Rica.
**Schizomitririum depressum** (Hedw.) Buck & Steere 8: 92280; 9: 92339, on rotten wood. - Carribbean.
**Schizomitririum grossiretis** (Bartr.) J. Florsch. 2: 92453, on soil.
**Schizomitririum pallidum** (Hornsch.) Crum & Anders. 1: 92110; 6: 92458; 8: 92291, on rotten wood.
**Schizomitririum radicans** (Besh.) Crum 9: 92340, on rock. - Carribbean.
**Schizomitririum rufescens** (Mitt.) J. Florsch. 2: 92142; 10: 92353, on wet rocks. - Neotropical.
*Thamniopsis killepiti* (Williams) Bartr. 3: 92165, 92170, on rotten wood. - Peru to Guyana. 
*Thamniopsis pendula* (Hook.) Fleisch. det. M.R. Crosby 2: 92149, on rotten wood.
THAMNOBRYACEAE det. J. Enroth 

*Porothamnium korthalsianum* (Dozy & Molk.) Mitt. (P. cobanense C. Müll.) 4: 92239. On rock. - Costa Rica, Panama.
*Porothamnium fasciculatum* (Hedw.) Fleisch. 5: 92255. On rock. - Neotropical.

THUIDIACEAE 

*Haplocladium microphyllum* (Hedw.) Broth. 1:92122; 3:92191; 8:92378, on soil, rotten wood and buttresses. - Cosmopolitan.
*Thuidium arceolatum* Lor. 4:92225; 5:92267, on rocks. - Neotropical.

BRACHYTHECIACEAE 


SEMATOPHYLLACEAE 

*Acroporiaceae* pungens* (Hedw.) Broth. 1: 92126, 92161, 92406; 2:92149; 3: 92409; 6: 92407; 7: 92408; 8: 92312; 8: 92297; 9: 92324; 9: 92406; 10: 92353. Frequent species on rotten wood, vertical small twigs and branches, especially in the canopy. So far only recorded from the Dept. of Chocó from one collection made by Steere. - Disjunct between the Neotropics and tropical Africa.
**Sematophyllum aff. sericifolium** Mitt. 3: 92163 on twig. Mexico, Cuba
**Sematophyllum subsimplex** (Hedw.) Mitt. 8: 92317 on buttress; 9: 92329 on rotten wood. - Neotropical.
*Taxithelium planum* (Brid.) Mitt. 6: 92454; 8: 92289. On rotten wood. - Neotropical.
*Taxithelium sp.* 9: 92329, on rotten wood. Differs from the
previous species by longer leaf tips. *Trichosteleum sp.*

1: 92127, on branch.

**HYPNACEAE**


**Ectropothecium apiculatum** (Hornsch.) Mitt. 1:92204. - South American.

*Mittenothannium reptans* (Hedw.) Card. 5: 92246. On rotten wood. -

In total, 358 specimens of mosses were collected at the ten plots studied. Of these, 85% (125 species) were named and are listed above. The evaluation is based on these 307 collections.

**Analysis of phytogeographical elements**

The evaluation of phytogeographical elements indicated in the list of species reveals the following composition (fig. 5):

The main phytogeographic element is the neotropical element with nearly 60% of species belonging to this group. It consists of usually widely distributed species ranging from southern Mexico to southern Brazil. Many of these species have a preference for more open habitats. Examples are *Octoblepharan cocuiense*, *O. stramineum*, *O. pulvinatum*, *Leucobryum martianum*, *Fissidens diplodus*, *F. guianensis*, *F. intramarginatus*, *F. mollis*, *Bryohumbertia filiformis*, *Hokomitrium fleuri*, *Calypnites azzelli*, *C. erosum*, *Syrhopodon circinatus*, *S. incompletus*, *S. leprieurii*, *S. lycopodioides*, *S. prolifer*, *S.

Pantropical, cosmopolitan and species disjunct between the Neotropic and tropical Africa count for another 12%, e.g. Polytrichum juniperinum, Leucobryum giganteum, Octoblepharum albivoltum, Hypophila involuta, Barbula indica, Pseudosmythiephora schimperi, Plagionorrhynchos rhynchosporium, Pyrrhobryum spiniforme, Racopilum tomentosum, Pilotrichella penispilosa, Halophiadium microphyllum, Palamocladium lespoides and Acrotrichum pungens.

The andine element is present with 6.6%. Examples are Campylopus asperifolius, C. huallagensis, Leucoloma procumbens, Didymodon laevigatus, Osculatta columbica, Rhizogonium mioidea and Cyclidiocystum corticatum.

The mesoamerican element with about 15% includes all species, which occur in Central America and northern South America and/or in the Caribbean but not in the Andes. Examples are Fissidens pelliculoides, F. weiri, Leucoloma mariae, Catenophyllopsis nigra, Splachnocris oxythrix, Leskeodendron longipilus, Callicostia fendleri, Cyclidiocystum lindigianum, C. rubrisetum, Hookeriospis obsoletinervis, Lepidoplium purpurascens, L. stolonaceum, Schizomium ciliariatum, S. depressum, S. grossretis, S. radicans, Porotrichium korthalsianum, P. lancifrons and Sematophyllum sericeofolium. These species can be regarded as lowland elements, which have spread from the Caribbean coast to the Pacific coast. This is possible since the Chocó region opens in the north with the flat valley of Rio Atrato. The valley is rather wide and low with elevations only up to 35 m, drains into the Caribbean Sea and and and provides and easy access for immigration of plants to the south. About 20% of moss species can be attributed to this element. There is no evidence that this valley was part of the Caribbean during past fluctuations of the sea level. The only transgression happened in this region 25 - 35,000 years ago was only a few feet and thus could not have influenced the Rio Atrato valley (Bartlett & Barghoorn 1973).

The composition of phytogeographical elements is much different in the single families. Pottiacceae, Mniumaceae, Rhizogoniaceae, Leucobryaceae, Rhacopilaceae include panropical elements. Fissidenaefceae, Calypseraceae, Braephaceae, Cryptaceae, Leucodontaceae, Priono- dontaceae, Trachypodaceae, Pterobryaceae, Meteoriaceae, Phyllogoniaceae, Neckeraeaceae include mostly neotropical species. The Hookeriaceae s.lat. (Leucomiaceae, Daltoniaceae, Callicostaceae) and Thamnobryaceae are the families with the most meso-american elements. The endemic element is represented with 3 species (=3.8%) species. According to Churchill (1991), ca. 100 species or 11% of the mossflora of Colombia are endemic.

There are 19 species of mosses indicated in the checklist by Churchill (1989), which are only known from one or more of the four departments of Colombia (Chocó, Cauca, Valle, Narino) belonging to the Chocó phytogeographical region. An evaluation of the distributional data using the database LATMOSS (C. Delgadillo M.) revealed that 16 are more widespread in the Neotropics, the Andes, Central America or the Caribbean. Only three (Lepidoplium permarginatum Williams, Octoblepharum costatum Crum in Maedegfau and Potanum recurvifolium Thér.) are presently known only from the Chocó region. It is, however, doubtful whether they are really endemic or synonymous with species described from elsewhere. Octoblepharum costatum Crum in Mädegfau was described as endemic to the Chocó region from a specimen collected by Mädegfau 1967.
Fig. 6: Phytogeographical elements of the mosses from six relevées.
near Quibdo. As pointed out in the comment under *O. cocuiense*, it may a synonym of the latter.

Endemic species found along the transect are *Fissidens cylindrothecus*, *Syrrhopodon isthmi* and *Holomitrium aberrans*. All these species have been described relatively recently, *Fissidens cylindrothecus* from the Chocó region, *Syrrhopodon isthmi* from Panama, *Holomitrium aberrans* in this paper. Conspicuously, all these species are epiphytic, which is commonly regarded as relatively young adaptation in evolution. The families involved are Fissidentaceae, Calypnaceae and Dicranaceae. The Fissidentaceae may be regarded as old group of bryophytes, of which, however, most of the species are terrestrial and only few have so far occupied ecological niches on stems and even canopy branches like *F. cylindrothecus*. Calypnaceae are predominantly epiphytes. This habitat preference as well as their very differentiated leaf structure indicates that these are comparably young branches in evolution. Also within the Dicranaceae, the tropical epiphytes can be interpreted as adaptations of extratropical, terricolous taxa to tropical rain forest habitats.

If the analysis of phytogeographical elements is made for single relevées, there are considerable differences in the composition of species at different altitudes (fig. 6). An edaphic element is only present in elevations between 1200 and 1800 m. Cosmopolitan species were only found between 1200 and 1600 m and near sea level. Pantropical species were also only present at higher altitudes between 800 and 1800 m. Neotropical species are represented at higher altitudes with 50-60% but below 500 m with 70-80%. Endemic species have been found at 100 and 200 m altitude, at 800, 1500 and 1600 m. This shows that the endemic element is not necessarily a lowland element. The most interesting element is the here called meso-american element. It illustrates the connections of the mossflora of the Chocó to the Central American and Caribbean region and seems bryologically the most specific characteristic of the Chocó mossflora. Six to eleven percent of meso-american species are found along the transect but fourteen just above sea level.

**Ecology, habitat preferences, habitat changes**

One of the most conspicuous effects in the bryophyte flora of the Chocó region is a change of habitats. Species which are found elsewhere on soil are growing epiphytic, and epiphytic species are found epiphyllous. For example, species of *Fissidens*, *Lepidopilum* and *Syrrhopodon* were found on leaves. This shift of habitats from soil to bark and from bark to leaves is attributed to the high humidity.

Another habitat change concerns species such as *Campylopus asperifolius*, which are usually found in the understory but occur in the canopy in the Chocó region.

**Altitudinal zonation**

The altitudinal zonation was evaluated by the determination of floristic discontinuities. For this purpose, the number of species with its lowermost or uppermost occurrence was calculated for each altitude (for the method used see also Gradstein & Frahm 1987). Base for this calculation were 44 species, which were found in more than one times and in more than one relevée. Highest floristic discontinuities were found at 200 m and at 1500 m (fig. 7). The upper limit at 200 m agrees quite well with the upper limit of the tropical lowland forest in the proposal of the altitudinal zonation of tropical rainforests by Frahm & Gradstein (1991) and also with the results of the study of the altitudinal zonation of tropical rainforests at the E-slope of the Andes in N-Peru based on the same method (Gradstein & Frahm 1987). The situation at these altitudes between 30 and 200 m in the present transect differs, however, by the higher number of species and higher percentage of cover. Both differences are interpreted as a result of the considerably higher precipitation in the Chocó region and also by the oceanity caused by the Pacific Ocean. It demonstrates very clearly that there is a specific floristic element in the lowland, which is usually not recognized in schemes of altitudinal zonations mostly for the reason that the studies on altitudinal zonation did not cover such low altitudes but started at higher altitudes.

Also the upper limit at 1500 m agrees perfectly
with the results of studies on altitudinal zonation based on floristic discontinuities in Peru (Gradstein & Frahm 1987) or estimation of percentage cover in Colombia (van Reenen & Gradstein 1984), phytomass of epiphytic bryophytes in Borneo (Frahm 1990). This altitude between 300 and 1500 m can be attributed to the tropical submontane forest, the relevées in 1600 and 1800 m to the lower tropical montane forest (Frahm & Gradstein 1991).

Examples for a wide altitudinal range between 30 and 1800 m are Acroporium pungens, Crossomitrium epiphyllum, C. patrigiae, Cyclidicyon albicans, Haplocladium microphyllum, Hyophila involuta, Isodrepanium lentulum, Leskeodon longipilus, Leucobryum martianum and Octoblepharum coueniense.

Lowland species limited to elevations to 30-200 m are Callicostia bipinnata, C. evansescens, Calymperes erosa, C. isthmi, Fissidens diplopus, F. intramarginatus, F. guianensis, Leucomium strunosum, Neckeropsis undulata, Octoblepharum albium, O. stramineum, Splachnobryum obtusum and Taxithelium planum.

Some species such as Octoblepharum pulvinatum and Orthostichopsis tetragona range from the lowland to 800 m.

Submontane species occurring between 300 and 800 (-1500) m are Bryum limbatum, Calymperes azzelli, Sylrophodon leprieurii, C. nicaraguense, Cyclidicyon rubristem, Fissidens mollis, Harpophyllum aureum, Hookeria crispa, Squamidium leucothrixum and Zelometeoryum patens.

Confined to elevations between 1500 and 1800 m are Bryobumherbia filifolia, Campylopous asperfolius, Fissidens asplenoides, F. polypodioides, Holomitrium flexuosum, Neophyrynella diversiifolia, Lepidogramum polyrrhizoides, L. stolonaceum, Leucobryum giganteum, Leucoloma ssp., Meteriospis remotifolia, Phyllogonium virede, Plagiomnium rhynchosporum, Polystichum juniperinum, Pyrrophytry um mnioides, P. spiniforme, Rhacophorum tomentosum, Rhodophyrum beyrichianum, Sphagnum merdum, Squamidium nigricans, Sylrophodon hycopodioides, S. prolifer, and Trachypus viridulus.

Species number per relevée

The number of mosses per relevée varies between 14 at 200 m and 39 at 1500 m. The relevées cannot really be compared, since they were more or less influenced by man, naturally composed (e.g. at 30 and between 1500 and 1600 m), partially logged (at 200 and 1800 m) or probably secondary (at 100 m). Nevertheless, a tendency can be recognized from the graph (fig. 8) illustrating the different species numbers along the transect. With the exception of the lowermost study site in a coastal forest at 30 m, there is generally an increase of species with the elevation, which can be observed also in other parts of the tropics. The influence of man is documented by the number of species in the way that the probably secondary forest at 100 m has only 14 mosses, whereas a less disturbed stand at 200 m has 23 species. The species number are around 20 in elevations between 400 and 700 m but increase to 28 and a maximum number of 39 in 1500 m. The decrease at 1600 seems to depend on the situation on a ridge and at 1800 m on logging.

Generic composition

Thirty-four species (=27%) of the 125 identified species along the transect belong to the Hookeriaceae s.l. (Hookeriaceae, Leucomiaceae, Daltoniaceae, Adelotheciaceae and mainly Callicostaceae), which is by far the largest family represented. Every fourth species belongs to this group. Already Herzog (1926) in his classical textbook indicated Colombia as diversity centre of Hookeriaceae. According to Churchill (1991a), the Callicostaceae with 16 genera and 80 species (Hookeriaceae s.lat. 24 genera with 106 species) are the second largest family in Colombia, only exceeded by the Di-ranaceae. Other families with high proportion are Calymperaceae and Leucobryaceae with 10 species (=8%), and Fissidentaceae and Meteorieaceae with 9 species (=7%). Sematophyllaceae are also represented with high numbers of species, but not fully identified.
Fig. 7: Floristic discontinuities along the transect studied.

Fig. 8: Numbers of species along the transect studied.
Delimitations of the Chocó phytogeographical region

The Chocó region was considered by Gentry (1982) to include "the coastal lowlands of western Colombia and northwest Ecuador". There are distinct limits to the S (Ecuadorian dry forest), W (Pacific Ocean), and E (Cordillera Occidental). Problematical seems to be the northern limits, which are given by Gentry (1982) with the Panamanian border. The inclusion of the coastal Pacific lowlands of Ecuador was originally based on the inventory of the Río Palenque area, an reserve of 167 ha in approximately 200 m above sea level (Dodson & Gentry 1978). This is the only undisturbed relictual coastal forest in Ecuador, of which the floristic composition is completely known. In 1988, the author had the opportunity to collect in the Río Palenque reserve. Although these collections do not represent a complete inventory, it allows to compare the species composition in this refuge with the relevés studied in the Chocó region of Colombia in a comparable altitude. This may not just be 200 m in Colombia but higher altitudes, because the Río Palenque area is situated in the influence of mist and cloud banks ("garua") caused by the cold Humboldt current, which causes a depression of the annual mean temperature, which resembles regions in 400-700 meters under normal climatic conditions.


Of these (although incomplete) list, all species with the only exception of *Fissidens neglectus* were found also along the transect studied in the Chocó region in Colombia. The Chocó phytogeographical element of flowering plants is primarily a lowland element (Gentry 1982). This could concern mosses, too. Of the three endemic moss species found along the transect, *Fissidens cylindrotheta* and *Syrhopodon isthmi* were collected below 200 m, only *Holomitrion aberans* (which is so far known only from the type locality and may prove to be an Andine element) in 1600 m. The Chocó region is known for its "high species diversity and strikingly high rates of endemism" amongst flowering plants and ferns (Gentry 1982). Endemism of flowering plants in the Chocó region is estimated by Gentry to 20%, 26% of the species occurring in the Río Palenque reserve are endemic to coastal Colombia and Ecuador.

High endemism concerns also pteridophytes, of which 15% of the species occurring in the Chocó department shall be endemic (Gentry 1982), which is an extraordinary high rate for spore plants. Even if the bryological exploration of the region is more complete, the percentage of endemic mosses cannot be expected as high. The Chocó region or at least the parts of it with extreme high precipitation have been regarded as Pleistocene refuge (Gentry 1982). Although Pleistocene refugia were considered for bryophytes (Frahm 1990), there is no evidence for it based on the relatively few collections of mosses made so far. Bryologically, in terms of mosses, the Chocó region can be defined as an extension of the Caribbean and Central American mossflora along the western side of the Western Cordillera in Colombia and northern Ecuador. This is easily to explain since the Chocó region drains to the Caribbean and is not separated from the lowlands of Panama. Although there is a small endemism, the rate of endemism is not significant higher than elsewhere.

Acknowledgements:
The fieldwork was made possible by a grant of the National Geographic Society (grant # 46 91-91). I like to thank J. Aguirre C., director of the Instituto de Ciencias Naturales,
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