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## Bryophyte diversity along an altitudinal gradient in Darién National Park, Panama

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**Abstract.** A bryophyte inventory along an altitudinal gradient on Cerro Pirre (1200 m), Darién National Park, Panama, demonstrates that the different rain forest types along the gradient (inundated-lowland, hillside-lowland, submontane, montane elfin forest) have very different species assemblages. The montane forest has the largest number of exclusive species and the largest bryophyte biomass. Species richness is greatest in the submontane forest.

The bryophyte flora of Cerro Pirre is not exceedingly rich in species owing to the rather low elevation of the mountain and the seasonal climate in the adjacent coastal plain. Nevertheless, the distinct altitudinal diversification and the occurrence of a considerable number of rare hepatic taxa, demonstrate the importance of Darién National Park as an area of plant conservation. Forty hepatic species are reported as new to Panama.

Darién National Park, created in 1980, is the largest nature reserve in the Republic of Panama and one of the largest in Central America. It is located in the Province of Darién along the border with Colombia and has a surface area of 579.000 hectares (Fig. 1). The park contains the largest hydrographic watershed in the country, that of the Tuira river and its tributaries. In 1981 the park was included in UNESCO's list of World Patrimonies and two years later, in 1983, it was declared a Reserve of the Biosphere.

The altitudinal gradient inventoried was located at Cerro Pirre (1200 m). This is the highest peak of the Serranía de Pirre, a mountain ridge located in the central portion of the park. The ridge extends northwards for about 35 kilometers from the Colombian border and is composed of Cretaceous igneous rocks (Myers 1969, Dalfelt and

Morales 1988). The climate of the area is humid-tropical, the mean annual temperature at the base of the mountain ranges between 22-25 degrees Celsius and the mean annual rainfall is over 2500 mm, with a pronounced dry season during January-April. Northern winds prevail from the end of December to April, while mild and variable southern winds predominate from May to December (Dalfelt and Morales 1978). A cooler climate with frequent clouds and mist occurs at the summit of Cerro Pirre. Virgin evergreen rain forest covers the slopes of the mountain and an elfin-type montane forest is found at the summit. The bryophyte flora of the Darién National Park is very poorly known. In recent years some bryophyte collecting in the park has been done by Panamanian and North American collectors but virtually nothing has been published on these



collections. The present study is the first one dealing with the bryophytes of the park.

Fieldwork was carried out by the authors during 4-8 June 1991 based on the INRENARE field station at the northwestern foot of Cerro Pirre, 4 km SE of the indian village of Pirre (Salazar 1989). Collections were made along the trail leading from the station to the summit, and along the path from the station to the town of El Real (Fig. 1). Five collecting sites were defined, as follows:

1. Trail El Real-Pirre, along Río Pirre, ca. 50 m. Cultivated lowland area with orchards, degraded woodland and isolated trees.
2. Periodically inundated lowland rain forest at the northwestern foot of Cerro Pirre, around INRENARE field station, ca 100 m. Palms are a conspicuous understorey element in this and the next forest type.
3. Hillside lowland rain forest on the lower slope and ridge of Cerro Pirre, along trail to Rancho Mojado, 400-500 m.
4. Submontane rain forest on the ridge to Cerro Pirre, above Rancho Mojado, 800-1100 m.
5. Montane cloud forest ("elfin forest") at the summit of Cerro Pirre, 1100-1200 m.

Sites 2-5 are located within the boundaries of Darién National Park and constitute the investigated altitudinal gradient on Cerro Pirre. Habitats inventoried include tree trunks from the base to 3 m above ground level, shrubs, lianas, vines, living leaves, decomposing logs, and soil. Some species were gathered from the crowns of fallen trees but an inventory of the forest canopy was not attempted.

About 200 collections were made, the majority of them hepatics. Even though mosses were much less prominent than hepatics at higher elevations, they are under-represented in the collections. In all, 124 species were collected, including 92 hepatics and 32 mosses (Table 1). Almost 90% of the species could be named; a few species of *Lejeunea* s.l. and *Plagiochila* and the moss genera *Acroporium*, *Isopterygium*, *Lepidopilum*,

*Macromitrium* and *Pirella* could not be identified. Identification of the mosses was carried out by Salazar Allen, of the hepatics by Gradstein with help from Dr R. Grolle (some species of *Lejeuneoideae* and *Tylimanthus*) and Dr K. Yamada (some species of *Radula*). The specimens have been deposited in the Herbarium of the University of Panama (PMA), with duplicates in the Herbarium of Utrecht University (U).

## Results and discussion

### Hepatics

#### Site 1. Cultivated lowland region, 0-50 m.

Fifteen species of hepatics were collected, including *Frullania gibbosa* Nees, *Radula flaccida* Lindenb. & Gott. and 13 species of *Lejeuneaceae* (Table 1). They are small corticolous species growing as appressed mats on the bark of fruit trees, treelets and shrubs in partial shade. All are widespread neotropical or pantropical species and most of them are xerotolerant taxa which are common in the canopy, in gaps and at the margins of primary rain forest, as well as in open, degraded habitats. One species collected here, *Frullanoides liebmanna* (Lindenb. & Gott.) van Slag., is new to Panama.

#### Site 2. Periodically inundated lowland rain forest, 100 m.

The hepatic flora in the forest understorey is poor and consists mainly of small, inconspicuous species which grow strongly attached to the bark of trees and on living leaves. Seventeen species were collected, including one species of *Plagiochila*, two of *Radula* and 14 *Lejeuneaceae* (Table 1). Epiphyllous taxa collected are *Cyclolejeunea convexistipa* (Lehm. & Lindenb.) Evans, *Radula flaccida* and *Taxilejeunea* sp. The corticolous species include several shade epiphytes characteristic of moist lowland rain forest in the neotropics: *Archilejeunea parviflora* (Nees) Schiffn., *Bryopteris filicina* (Sw.) Nees, *Echinocolea asperrima* (Spruce) Schust., *Radula kegelii* Gott. ex Steph., *Prionolejeunea muricata-serrulata* (Spruce) Steph., *Stictolejeunea*

*squamata* (Willd.) Schiffn. and *Symbiezidium barbiflorum* (Lindenb. & Gott.) Evans. All are widespread neotropical taxa, except for *Echinocolea asperrima*, *Radula kegelii* and *Prionolejeunea muricato-serrulata* which are South American species new to Panama.

### Site 3. Hillside lowland rain forest, 400-500 m.

The forest understorey on the lower slopes of Cerro Pirre, between 200-400 m, is very poor in bryophyte species but on the ridge towards the summit of a hill (500 m), before reaching Rancho Mojado, a more diversified hepatic flora occurs. The 21 species collected here include *Calypogeia miquelii* Mont., *Micropterygium pterygophyllum* (Nees) Trevis., *Plagiochila exesa* Lindenb. & Gott. and 18 Lejeuneaceae (Table 1). The species grow on bark or living leaves except *Calypogeia miquelii* which inhabits bare soil. The corticolous bryophyte flora is rich in species of *Ceratolejeunea* (*C. cornuta* (Lindenb.) Schiffn., *C. laetefusca* (Aust.) Schust., *C. patentissima* (Hampe & Gott.) Evans, and *C. spinosa* (Gott.) Steph.) while two species of *Cyclolejeunea*, *C. convexistipa* and *C. peruviana* (Lehm. & Lindenb.) Evans, are common on leaves. All species are rather widespread neotropical taxa except for *Calypogeia miquelii* and *Micropterygium pterygophyllum*, which are South American species new to Panama.

### Site 4. Submontane rain forest, 800-1100 m.

The submontane forest above 800 m is much richer in epiphytic bryophytes, in terms of number of species and biomass, than the lowland forest and harbours a very different hepatic flora. The slightly lower and more open forest canopy on the steep ridge, the lower air temperatures and the increased humidity due to more frequent clouds at these elevations are factors probably responsible for the changes in the vegetation. The submontane forest is transitional to the summit forest as is indicated by the increase in importance of species of *Plagiochila* and *Bazzania* and the decrease of Lejeuneaceae.

A total of 38 hepatic species were collected, including 26 Lejeuneaceae (Table 1). Many of them are new to Panama. The two species of

*Bazzania* found in the submontane forest, *B. hookeri* (Lindenb.) Trevis. and *B. stolonifera* (Sw.) Trevis., were also common in the cloud forest but the *Plagiochila* species, *P. vincentina* Lindenb. and *P. dubia* Lindenb. & Gott., were only found in the submontane forest. Further species characteristic of the submontane forest and not found elsewhere include *Ceratolejeunea fastigiata* (Spruce) Steph., *Cystolejeunea lineata* (Lehm. & Lindenb.) Evans, *Echinocolea dilatata* (Evans) Schust., *Harpalejeunea stricta* (Lindenb. & Gott.) Steph., *Luteolejeunea herzogii* (Buchloh) Piippo, *Pictolejeunea picta* (Gott. ex Steph.) Grolle, *Prionolejeunea macrocardia* (Spruce) Steph., *P. trachyodes* (Spruce) Steph. and *Radula saccatiloba* Steph. on bark, and the epiphyllous *Cyclolejeunea chitonia* (Tayl.) Evans, *Diplasiolejeunea cavifolia* Steph. and *D. brunnea* Steph.

*Fulfordianthus pterobryoides* (Spruce) Gradst., a robust dendroid lejeuneaceous species was very common on the lower bases of tree trunks. A small form of the species occurred scattered on the top of the hill at 500 m. *Fulfordianthus pterobryoides* is a "Chocó element" occurring along the Pacific side of the continent from Ecuador to Costa Rica (Gradstein 1992). Other species of the submontane forest with restricted geographical distributions include *Cystolejeunea lineata* (Caribbean element) and *Luteolejeunea herzogii* (Chocó element).

### Site 5. Montane cloud forest at the summit, 1100-1200 m.

The summit of Cerro Pirre is covered by montane "elfin forest", characterized by a very low (ca 5-10 m) and open canopy and an abundant epiphytic vegetation. Frequent clouds, mist and strong winds are important climatic factors at this elevation. The biomass of the epiphytic bryophytes, virtually all of them hepatics, is dramatically greater than at lower altitudes. Thirty two species of hepatics were collected, of which only 13 are Lejeuneaceae (Table 1). Almost half of the species are new to Panama. In the montane forest Lejeuneaceae are no longer an important element of the flora. Most of them are tiny species which produce very little biomass. The important epiphytic hepatics which produce most of the epiphytic biomass include

*Bazzania hookeri*, *B. stolonifera*, *Calypogeia lechleri* (Steph.) Steph., *Herbertus divergens* (Steph.) Herz., *Lepidozia patens* Lindenb., *Metzgeria albinea* Spruce, *Plagiochila adianthoides* (Sw.) Dum., *P. rutilans* Lindenb., *Symphogyna brasiliensis* Nees and *Trichocolea tomentosa* (Sw.) Gott. An undetermined, probably new species of *Plagiochila*, characterized by strongly caducous untoothed leaves, was also very abundant. On roots and rotten wood *Cephalozia crassifolia* (Lindenb. & Gott.) Fulf. and two species of *Riccardia*, *R. fucoidea* (Sw.) Schiffn. and *R. cervicornis* (Spruce) Herz. ex Gradst. & Hekking, were frequently encountered. Common epiphyllous hepatics of the montane forest include *Cyclolejeunea convexistipa*, *Drepanolejeunea inchoata* (Meiss.) Steph., *D. lichenicola* (Spruce) Steph., *D. pinnatiloba* Schiffn., *Odontolejeunea lunulata* (Web.) Schiffn. and *Prionolejeunea aemula* (Gott.) Evans.

All of the above-mentioned species are exclusive to the montane forest, except for the two *Bazzania* species which are also in the submontane forest, and *Cyclolejeunea convexistipa* which occurs along the entire slope of the mountain and is one of the most common hepatics of Cerro Pirre.

The following species of the montane forest have restricted geographical distributions: *Calypogeia lechleri*, *Ceratolejeunea dentato-cornuta* Steph. and *Riccardia cervicornis* (South American species), *Lepidozia patens* (Caribbean species) and *Plagiochila rudischusteri* Robins., a species recently described from Venezuela (Robinson 1988).

### General conclusions on the hepatic diversity of Cerro Pirre

In all, 86 species of hepatics were collected in the rain forest of Cerro Pirre (sites 2-5), within the boundaries of Darién National Park. An additional six species (*Frullania gibbosa*, *Caudalejeunea lehmanniana*, *Mastigolejeunea auriculata*, *Cheilolejeunea rigidula*, *Diplasiolejeunea rigidula*, *Lejeunea laetevirens*) were found in the cultivated land between El Real and Pirre, beyond the limits of the park. The latter species are common, xerotolerant epiphytes of forest margins and open, secondary habitats, and usually lack in

the shaded understorey of the virgin forest (Cornelissen and Gradstein 1990). On Cerro Pirre they may occur in the canopy of the forest, which was not inventoried in this study.

Species diversity and biomass of hepatics changed considerably along the altitudinal gradient. The lowland forest sites (2, 3) had 19 species on average, the submontane forest had 37 species and 32 species were found in the montane elfin forest. Only 13 species (17%) were shared by the lowland and the submontane forest and only 7 species (11%) were common to the submontane forest and the montane forest. Furthermore, almost half of the species found in the lowland and submontane forest were exclusive to either of these forest types. Twenty two species (almost 70%) occurred exclusively in the montane forest. The figures may be somewhat biased by incomplete sampling, yet give a first impression of the species diversity along the altitudinal gradient of Cerro Pirre.

It thus appeared that the montane forest had more unique species than the other forest formations of Cerro Pirre. The hepatic biomass in the montane forest, moreover, is much greater than at lower altitudes, due to the prevalence of fog at the summit. Species richness, however, is greatest in the submontane forest which is somewhat transitional between the lowland and the montane forest, both in terms of species composition and biomass.

Fifty nine hepatic species or about 65% are members of the Lejeuneaceae, which is by far the most important bryophyte family in the area. In the lowland rain forest (inundated and hillside together) species of Lejeuneaceae account for more than 80% of the hepatic flora; in the rich submontane forest 60% and in the montane forest only 40%. Most of the lejeuneaceous species are tiny plants which produce little biomass. The large epiphytic biomass in the elfin forest is almost entirely produced by the non-lejeuneaceous genera *Bazzania*, *Plagiochila*, *Herbertus*, *Calypogeia* and *Trichocolea*.

Forty hepatic species new to Panama were collected; previously almost 200 species had been reported from the country (Dr. R. Stotler, personal communication). Thus, the number of hepatic species known from Panama has increased almost 20% as a result of our investigation. The new

species are marked by an asterisk in Table 1. Furthermore, several rare taxa with restricted geographical distributions were found, including *Plagiochila rudischusteri* previously known only from northern Venezuela, *Ceratolejeunea dentato-cornuta*, *Echinocolea asperrima* and *Micropterygium pterygophyllum* from South America, the Caribbean *Cystolejeunea lineata* and *Echinocolea dilatata*, and the Chocó elements *Fulfordianthus pterobryoides* and *Luteolejeunea herzogii*. An undescribed species of *Plagiochila* was one of the dominant species in the elfin forest. The unusual species are highlighted in **bold** in Table 1.

The hepatic flora of Cerro Pirre is not exceedingly rich in species compared with areas elsewhere in the neotropics, probably due to the low altitude of the mountain and the prolonged dry season in the adjacent coastal plain of Darién province. Nevertheless, the distinct altitudinal diversification of the flora and the occurrence of a rather large number of rare taxa exemplify the importance of Darién National Park as an area of plant conservation.

### Mosses

Few mosses were collected compared to hepatics. Most of those found had a large altitudinal range, occurring from lowland to submontane forest over 1000 m. Thirty two species in sixteen families were identified. A survey of the collections in the University of Panama herbarium added a further five species to the list, based on material collected in the area by staff of the Missouri Botanical Garden (Table 1).

There is a slight predominance of pleurocarps (21 spp.) over acrocarps (16 spp.) in the moss flora of Cerro Pirre. The most important families in number of species are Calymperaceae (11), Hookeriaceae (6 or more), Pterobryaceae (3) and Sematophyllaceae (3). All lowland species (0-100 m) in Pirre are common to Barro Colorado Island, Panama, except *Leucophanes molleri* C. Müll. and *Syrrhopodon prolifer* Schwaegr. However, the moss flora of Barro Colorado (Salazar Allen et al. 1991) has a higher number of hookeriaceous taxa and Fissidentaceae are well represented whereas no collections of *Fissidens* were made in Pirre.

The same number of species of Calymperaceae (11) were found in Pirre and Barro Colorado but only five of them are common to both places. The other six include some elements characteristic of cloud forest of higher elevations. Four of the eleven species of Calymperaceae are pantropical in distribution (*Calymperes afzelii* Sw., *C. lonchophyllum* Schwaegr., *Octoblepharum albidum* Hedw. and *Syrrhopodon prolifer*), whereas the rest are neotropical elements. As elsewhere in tropical rain forests (Reese 1961, 1991), the species of *Calymperes* are found at low elevations (sea level to 500 m) whereas *Syrrhopodon* is more common at higher elevations. Distinct altitudinal diversification is also seen among the species of *Octoblepharum* (Salazar Allen 1991). Thus, *O. albidum* and *O. pulvinatum* (Dozy et Molke.) Mitt. are common lowland species (although they can also grow in forest above 1000 m in Central America), whereas *O. cucuiense* Mitt. and *O. erectifolium* Mitt. are elements of montane cloud forest.

Members of the Hookeriaceae appear above 400 m and are also present at higher elevations. They are the second family in importance above 800 m, but are nearly absent in the lowlands. In the forests of Fortuna (Chiriquí, Panama, 900-1500 m) Hookeriaceae are the most important moss family in numbers of species (Salazar Allen, unpublished). On Cerro Pirre, however, the Calymperaceae appear to be dominant, followed by the Hookeriaceae.

Phytogeographically, the moss flora of Pirre contains many elements widely distributed in Central America, the Caribbean and tropical South America. Pantropical species are also common and include *Calymperes afzelii*, *C. lonchophyllum*, *Neckeropsis disticha* (Hedw.) Kindb., *Octoblepharum albidum*, *Pyrrhobryum spiniforme* (Hedw.) Mitt. and *Syrrhopodon prolifer*. Some elements are common to the African flora, like *Cyrtohypnum involvens* (Hedw.) (= *Thuidium involvens* (Hedw.) Mitt.), *Leucophanes molleri* and *Taxithelium planum* (Brid.) Mitt. The Afro-American species are most probably acquisitions from the rich South American moss flora (Salazar Allen 1986).

The above observations on the mosses of Cerro Pirre are preliminary. More material is needed to determine whether the floristic trends observed

reflect local differences in environmental and/or geological factors or are simply the products of under-collecting.

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