

EPIPHYLLOUS BRYOPHYTES FROM COCOS ISLAND, COSTA RICA. A FLORISTIC AND PHYTOGEOGRAPHICAL STUDY

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Resumen. Se estudió la flora y fitogeografía de briófitos epífilos de la Isla del Coco (Costa Rica). Con un total de 45 especies de epífilos, incluyendo 9 registros nuevos, el número total de especies de briófitos encontrados aumenta a 162, de las cuales 56 son musgos y 106 son hepáticas. La flora de los briófitos epífilos de la Isla del Coco tiene una afinidad fitográfica a la unidad neotropical. Casi todas las especies ocurren en América Central o en el norte de Suramérica. Muchas de las especies (30 de 45) epífilas son raras en la Isla del Coco y solamente están presentes en pocos forófitos. En la zona montañosa de la isla, los briófitos epífilos frecuentemente crecen en el lado inferior de las hojas. La diversidad, distribución y densidad de los briófitos epífilos es diferente entre los sitios investigados y parece depender de diferencias microclimáticas, especialmente humedad, pero también corresponde en cierto grado a la diversidad de la vegetación del entorno.

Abstract. Epiphyllous bryophytes of Cocos Island (Costa Rica) were studied with respect to their floristics and phytoecography. With a total of 45 epiphyllous species observed, including 9 new records, the total number of bryophytes found on Cocos Island increases to 162, 56 mosses and 106 liverworts. The epiphyllous bryophyte flora shows phytoecographical affinities mainly to the Neotropics, and nearly all species occur in Central or northern South America. Many of the epiphyllous bryophytes (30 out of 45) are rare on Cocos Island, and only present on a few phorophytes. In the mountainous area epiphyllous bryophytes frequently grow on the underside of the leaves. Species diversity, distribution and density differ between the investigated sites and seem to depend mainly on microclimatic conditions, especially humidity, but also correspond to a certain degree to differences in the vegetation diversity. *Accepted 13 April 2000.*

Key words: Epiphyllous bryophytes, diversity, floristic, phytoecography, Cocos Island, Costa Rica, tropical rainforest.

INTRODUCTION

Cocos Island is situated in the Pacific Ocean between mainland Central America and the Galápagos Islands. Politically the island belongs to Costa Rica. It was made famous worldwide by R. L. Stevenson (1883) in the story "Treasure Island". In fact, treasures estimated at about US \$ 800 million are said to be hidden on the island (Diesch-Lauxmann 1985; Weston 1990, 1992) but in spite of intensive searching almost nothing has been found. The real treasure of Cocos Island is its natural beauty and unique biology.

The spermatophytes, ferns and fungi (Stewart 1912; Fournier 1966; Gómez 1975a, b, 1983) and foliicolous lichens (R. Lücking & A. Lücking 1995) of Cocos Island are relatively well known, and bryophytes have been studied by Stewart (1912), Barrtram (1933), Howe (1934) and Clark (1953). A synthesis of these studies was made by Fosberg & Klawe (1966), resulting in a total number of 25 species of

mosses and 27 liverworts. But due to poor collecting, especially of liverworts, the total number of bryophyte species was underestimated. A recent collection of corticolous and terrestrial bryophytes (Dauphin 1995, 1999) yielded a large collection of bryophytes, recording a total number of 153 species, 54 mosses and 98 liverworts, and one hornwort. However, epiphyllous taxa were not taken into consideration.

Epiphyllous bryophytes grow on the surface of living leaves of higher plants, forming communities with foliicolous lichens and some algae (Vareschi 1980, Richards 1984). These leaf-inhabiting organisms are regularly epiphytic and only a very few are parasites, therefore the host plants are called phorophytes. The highest species diversity of epiphyllous bryophytes is found in tropical rainforests. Nearly all species are liverworts belonging to the large family Lejeuneaceae. Some species belong to the genera *Metzgeria* (Metzgeriaceae) and *Radula* (Radulaceae). Only a few species of mosses, belonging mainly to the genus *Crossomitrium* (Hookeriaceae), grow regularly and frequently on living leaves.

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In April 1992, I collected epiphyllous bryophytes on Cocos Island and investigated their flora and ecology. I studied their phylogeographical affinities, species diversity, distribution and density at different sites at Cocos Island. In this paper I also consider how geographical location, climate, topography and vegetation type of the different island sites affect the epiphyllous bryophyte flora.

MATERIALS AND METHODS

Study area. Cocos Island is situated in the Pacific Ocean, latitude 5°N and longitude 87°W, c. 500 km southwest of Costa Rica and c. 800 km northeast of the Galápagos Islands (Fig. 1). The island, which is of volcanic origin (Chubb 1933), has never been connected to the continent (Stewart 1912) and is characterized by a very irregular topography. The climate is influenced by the Intertropical Convergence Zone, which shifts from north to south and back. From April to December the island is in the path of the eastward flowing Equatorial Countercurrent, thus prevailing winds are from the southwest. In January the Intertropical Convergence Zone is displaced to the south and Cocos Island comes under the influence of westward directed currents and winds from off the mainland of Central America and northern South America (Hertlein 1963, Montoya 1988, 1990). Annual rainfall totals up to 7000 mm (Herrera 1985, Montoya 1990) leading to an exceptional tropical rainforest flora and fauna.

Gómez (1975a, b) and Montoya (1990) distinguished three different vegetation zones: the littoral zone (0–50 m a. s. l.), the montane zone (100–630 m), and the transitional zone (50–100 m). The littoral zone comprises the bays and their narrow valleys. Here, the dominant species are *Cocos nucifera* L. and *Annona glabra* L., many epiphytic Bromeliaceae and Orchidaceae, and Poaceae, Fabaceae, and Malvaceae in the understory. In the montane zone, *Saccoglottis holdridgei* Cuatrecasas, Arecaceae, and Lauraceae are predominant and a rich and diverse bryophyte and fern flora is present. The transitional zone is a mixed vegetation of Melastomataceae and Lauraceae.

Cocos Island is of more recent origin than the adjacent Galápagos Islands, with fewer species of higher plants (Hertlein 1963, Fournier 1966). The rate of endemism of about 10% is much lower than that of the Galápagos Islands, at about 40% (Stewart 1912, Fournier 1966, Lawesson *et al.* 1987). The vegetation of Cocos Island is most similar to that of

Central or South America (Fournier 1966; Gomez 1975 a, b, 1983; Gradstein & Weber 1982).

Study sites. Epiphyllous bryophytes were collected at 11 different sites on Cocos Island along a transect running from NE to SW (Fig. 1). The sites are located along the trails from Chatham to Wafer Bay and from Wafer Bay to the top of Cerro Iglesias; Iglesias Bay was reached by boat. Following my observations, the classification of the vegetation zones given by Gómez (1975a, b) and Montoya (1990) was modified, taking differences in vegetation types and altitude into consideration. Four different vegetation zones were distinguished: open littoral vegetation (0 m = OL), lowland forest (0–100 m = LF), lower mountain forest (100–250 m = LM), and upper mountain forest (250–630 m = UM). For each zone three sites were chosen, except for the open littoral vegetation which is represented only by two sites. The sampled sites are as follows:

Chatham Bay (1): Narrow strip of littoral vegetation behind the beach (0 m altitude, OL). *Cocos nucifera* L., *Terminalia catappa* L., and *Hibiscus tiliaceus* L. are the typical elements. The adjacent steep cliffs are characterized by a low vegetation with *Commelina diffusa* Burm. and various species of ferns.

Colnett Peninsula (2): Plateau along the first part of the trail from Chatham to Wafer Bay (200–250 m, LM). The tree layer is dominated by *Saccoglottis holdridgei*, which is frequently inhabited by epiphytic bromeliads of the genus *Guzmania*. The understory is very open and composed mainly of *Hypolytrum amplum* Poeppig & Kunth, a species of Cyperaceae widely distributed in this area by the digging activities of pigs introduced on the island.

Presidio Peninsula (3): Second steep and rocky part along the trail from Chatham to Wafer Bay (100–200 m, LM). The tree layer is dominated by *Ocotea insularis* (Meissn.) Mez. and *Cecropia pittieri* Robinson. The understory is composed mainly of Melastomataceae and the terrestrial ferns *Danaea nodosa* (L.) J.E.Sm. and *Polybotrya cervina* (L.) Kunze.

Wafer Bay (4): Littoral vegetation (0 m, OL) including several vegetation types. The beach vegetation is characterized by *Hibiscus tiliaceus*, *Cocos nucifera*, *Terminalia catappa*, and *Ipomoea pes-caprae* (L.) Sweet. Influenced by the range of the tides, the vegetation is similar to mangroves and is dominated by the trees *Annona glabra* L., *Cassipourea guianensis* Aublet, and *Conocarpus erectus* L. The fern *Acrostichum aureum* L. is common in the understory. Around the ranger

station a small tract of land has been cultivated with introduced plants like *Musa* sp., *Citrus* sp., *Mangifera indica* L., and *Delonix regia* Rafin.

Río Genio (5): Lower part of the river along the river banks (0–50 m, LF). The vegetation is characterized by *Ardisia compressa* H.B.K. Young plants of *Ocotea insularis* and several shrubs of the family Melastomataceae are common in the understory as well as the terrestrial ferns *Danaea nodosa* and *Polybotrya cervina*.

Iglesias A (6): First steep and rocky part of trail from Wafer Bay to Cerro Iglesias (50–100 m, LF).

The vegetation is similar to that found at Río Genio (5) but the understory is denser and with fewer terrestrial ferns.

Iglesias B (7): Small plateau on the second part of the trail from Wafer Bay to Cerro Iglesias (150–250 m, LM). The montane vegetation is similar to that of Presidio Peninsula (3).

Iglesias C (8): Third part of the trail from Wafer Bay to Cerro Iglesias (250–350 m, UM). The tree layer is dominated by *Saccoglottis holdridgei* and *Ocotea insularis*, which are frequently covered with epiphytic Bromeliaceae (*Tillandsia* and *Guzmania*). The

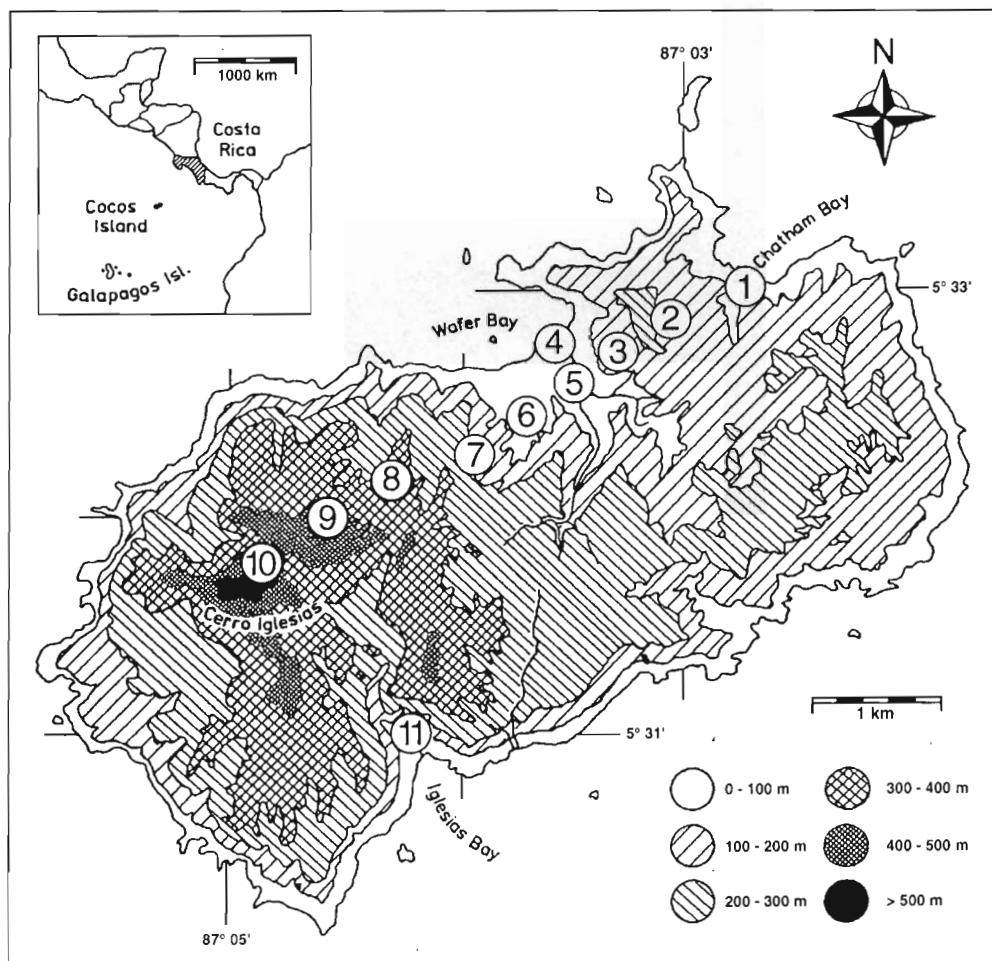


FIG. 1. Geographical position and topography of Cocos Island and the investigated sites. (1) Chatham Bay, (2) Colnett Peninsula, (3) Presidio Peninsula, (4) Wafer Bay, (5) Río Genio, (6) Iglesias A, (7) Iglesias B, (8) Iglesias C, (9) Iglesias D, (10) Cerro Iglesias, (11) Iglesias Bay.

understory is dense and characterized by Melastomataceae.

Iglesias D (9): Fourth part of the trail from Wafer Bay to Cerro Iglesias (350–500 m, UM). The vegetation is similar to that of Iglesias C (8) but with *Euterpe macrospadix* Oersted intermingled in the tree layer. There are fewer bromeliads and increasing cover of epiphytic bryophytes. The understory is characterized by tree ferns.

Cerro Iglesias E (10): Last part of the trail from Wafer Bay to the top of Cerro Iglesias (500–634 m, UM). The elfin forest vegetation is lower and mainly composed of *Saccoglottis holdridgei*, *Euterpe macrospadix*, and many tree and terrestrial ferns. Epiphytic bryophytes occur in thick layers.

Iglesias Bay (11): Lower part of the Río Pittier along the river banks to the waterfall (0–20 m, LF). The vegetation is similar to that found at Río Genio (5) but the understory is more exposed and there are fewer terrestrial ferns. The ground is very irregular because of previous treasure hunting which has left many hollows about 2–4 m in diameter.

Sampling. A total of 57 phorophyte plants belonging to the 23 commonest or most typical species of the vegetation were sampled. Leaves were collected randomly at each site, from a height of up to 2 m along a transect marked by the trail and extending about 5 m into the forest. It was not possible to collect leaves from the same species of phorophytes at each site because of the differences in the vegetation type. Therefore collection lasted until no more new species were found within 30 minutes (an estimated one hour of collection activity per site).

The phorophytes were: *Danaea nodosa* (L.) J. E. Sm. (Marattiaceae), *Acrostichum aureum* L. (Pteridaceae), *Elaphoglossum* sp. (Lomariopsidaceae), *Polybotrya cervina* (L.) Kunze, *P. osmundacea* H. B. ex Willd., *P. polybotryoides* (Baker) Christ (all Dryopteridaceae), *Cocos nucifera* L. (Arecaceae), *Spathiphyllum* sp. (Araceae), *Philodendron* sp. (Araceae), *Annona glabra* L. (Annonaceae), *Saccoglottis holdridgei* Cuatrec. (Humiaceae), *Ocotea insularis* (Meisn.) Mez (Lauraceae), *Coffea arabica* L. (Rubiaceae), *Citrus* sp. (Rutaceae), *Calophyllum brasiliense* Cambess. (Clusiaceae), *Mangifera indica* (Anacardiaceae) and a few species of Melastomataceae that were identified only to family level.

Epiphyllous bryophytes were identified by comparison with original descriptions and type material. For some species the keys by Gradstein (1989, 1994), Schuster (1958, 1980), Castle (1939) (*Radula*), and

Allen (1990) (*Crossomitrium*) were used. Specimens are deposited at the herbaria of the University of Costa Rica (USJ) and The University of Ulm (ULM), as well as in the private herbarium of the author.

Ecogeographical analysis. STATISTICA (Release 4.5 for Windows, StatSoft, Inc., 1993) was used for all analyses. Because normal distributions could not be assumed for the data sets, non-parametric tests were applied. Frequency distribution of epiphyllous bryophytes was calculated using presence-absence data. Classes were established by repeat calculations of 50%, starting with the total number of the 57 investigated phorophytes.

Diversity of epiphyllous bryophytes at the different sites was measured as α -diversity or "richness-diversity" (Whittaker 1972, 1977; Magurran 1988). Sites were compared with the chi-square-test.

Samples of epiphyllous bryophytes at different sites only represent part of the community which is actually present. The expected true species richness was estimated using the Jackknife Estimate (Krebs 1989), which is based on the observed frequency of unique species in the community:

$$\hat{S} = S + [(n - 1) / n] k$$

where \hat{S} = Jackknife Estimate of species richness, S = observed number of species present on n phorophytes, n = total number of phorophyte plants, k = number of unique species (i.e., number of species only present on one phorophyte). Variation in species richness between sites was compared with the coefficient of variation (CV), calculated as the quotient of the Jackknife Estimate and its standard deviation (Krebs 1989).

A cluster analysis of the sites was carried out, based on species composition of epiphyllous bryophytes. The similarity matrix was performed using the Sørensen Index (Sørensen 1948), after Lücking (1994). The linkage rule was the "weighted pair-group average". The vegetation type and microclimatic conditions of the resulting groups were compared.

RESULTS

Floristics. Forty-five species of epiphyllous bryophytes were found on Cocos Island (Table 1), seven of which are new records, thus increasing the total number of bryophyte species on Cocos Island to 160, 55 mosses, 104 liverworts, and one hornwort. Epiphyllous bryophyte species represent about 10% of all plants and fungi, about 30% of all bryophyte species, and 40%

TABLE 1. List of epiphyllous bryophytes of Cocos Island, their vegetative propagation and geographical distribution (from Gradstein & Weber 1982, Dauphin 1995, Pócs pers. comm. and personal observations). Species new to Cocos Island are marked with an asterisk (*). All collections were made by the author. Selected specimens are cited only with collection numbers.

Hepaticae:

Aphanolejeunea camillii (Lehm.) R. M. Schust. – Neotropical, discoid gemmae. Bahia Iglesias, 615 (hb. Bernecker).

Aphanolejeunea costaricensis A.Lücking – Caribbean, Central American, northern South American, discoid gemmae. Bahia Iglesias, 614 (ULM), 618 (UCR), 457 (hb. Bernecker); Río Genio, 502 (hb. Bernecker).

* *Aphanolejeunea cyathiphylla* Herzog – Neotropical, discoid gemmae. Bahia Iglesias, 462 (hb. Bernecker), 614 (ULM); Iglesias D, 621 (UCR); Río Genio 501 (hb. Bernecker).

Aphanolejeunea sicaefolia (Gottsche) A. Evans – Neotropical, Galápagos Islands, discoid gemmae. Iglesias E, 307 (hb. Bernecker).

Aphanolejeunea sp.1 – discoid gemmae. Río Genio, 515, 521, 538 (hb. Bernecker).

Aphanolejeunea sp. 2 – discoid gemmae. Iglesias A, 362 (hb. Bernecker).

* *Ceratolejeunea* cf. *dentatocornuta* Steph. – northern South American (Ecuador). Río Genio, 550 (hb. Bernecker).

Ceratolejeunea plumula (Spruce) Steph. – Neotropical. Bahia Iglesias, 456 (ULM), 462 (hb. Bernecker), 471 (UCR); Río Genio, 520 (ULM), 544 (UCR), 262 (hb. Bernecker).

Ceratolejeunea rubiginosa Steph. – Neotropical. Bahia Iglesias, 464 (UCR); Iglesias B, 292 (hb. Bernecker); Río Genio, 509 (ULM).

Cheilolejeunea adnata (Kunze) Groll – Neotropical. Iglesias C, 285 (hb. Bernecker); Río Genio, 284 (UCR).

Cheilolejeunea decurvuloba (Steph.) He – Neotropical. Iglesias E, 312, 313 314 (hb. Bernecker), 314 (UCR).

Cheilolejeunea cf. *rigidula* (Mont.) R. M. Schust. – Neotropical and African. Iglesias B, 571 (hb. Bernecker); Río Genio, 510 (UCR), 545 (hb. Bernecker).

Cololejeunea cardiocarpa (Mont.) Steph. – Pantropical, Galápagos Islands, discoid gemmae. Wafer Bay, 647 (hb. Bernecker), 491 (UCR), 494 (ULM).

Cololejeunea submarginata Tixier – Neotropical, discoid gemmae. Iglesias A, 273 (ULM), 274, 681 (hb. Bernecker), 685 (UCR); Presidio, 275, 450 (hb. Bernecker), 652 (UCR), 653 (ULM).

Colura tortifolia (Mont.) Steph. – Neotropical, discoid gemmae. Río Genio, 352 (ULM), 353 (UCR), 350 (hb. Bernecker).

* *Colura cylindrica* Herzog – Neotropical, Galápagos Islands, discoid gemmae. Iglesias A, 354 (UCR, hb. Bernecker); Río Genio, 356 (ULM).

* *Colura greig-smithii* Jover-Ast – Trinidad (Caribbean), Guianas, discoid gemmae. Iglesias A, 360 (hb. Bernecker); Presidio, 358 (UCR); Río Genio, 361 (hb. Bernecker).

Cyclolejeunea accedens (Gottsche) A. Evans – Neotropical, discoid gemmae. Iglesias E, 307, 609, 710 (hb. Bernecker), 616 (UCR).

Cyclolejeunea convexistipa (Lehm. & Lindenb.) A. Evans – Neotropical, discoid gemmae. Bahia Iglesias, 468, 469, 473 (hb. Bernecker), 472 (ULM), 503 (UCR).

Cyclolejeunea luteola (Spruce) Groll – Neotropical, discoid gemmae. Iglesias E, 710 (hb. Bernecker).

Cyclolejeunea peruviana (Lehm. & Lindenb.) A. Evans – Neotropical, discoid gemmae. Iglesias E, 706, 707 (hb. Bernecker).

Cystolejeunea lineata (Lehm. & Lindenb.) A. Evans – Neotropical. Iglesias E, 283 (UCR), 363, 708 (hb. Bernecker).

* *Diplasiolejeunea inermis* Tixier – Neotropical, discoid gemmae. Bahia Iglesias, 470 (UCR), 467, 689 (hb. Bernecker), 624 (ULM); Colnett, 455 ULM, 625 (hb. Bernecker), 704 (UCR); Iglesias A, 558, 629, 681 (hb. Bernecker), 680 (UCR), (699) ULM.

Diplasiolejeunea pellucida (C.F.W. Meissn.) Schiffn. – Neotropical and African, discoid gemmae. Iglesias A, 326 (ULM), 630, 671 (hb. Bernecker), 694 (UCR); Wafer Bay, 634 (hb. Bernecker), 670 (ULM), 678 (UCR).

- Drepanolejeunea crucianella* (Taylor) A. Evans – Neotropical, brood branches. Iglesias D, 583, 584, 587 (hb. Bernecker); Iglesias E, 642 (UCR); Río Genio, 517 (ULM).
- Drepanolejeunea inchoata* (C.F.W. Meissn.) Steph. – Neotropical, Galápagos Islands, brood branches. Iglesias A, 563 (hb. Bernecker); Iglesias C, 580 (UCR); Río Genio, 536 (UCR), 517 (ULM).
- * *Harpalejeunea* sp. Iglesias B, 572 (hb. Bernecker).
- Lejeunea flava* (Sw.) Nees – Pantropical, Galápagos Islands. Iglesias D, 589 (hb. Bernecker); Río Genio, 500 (UCR).
- Lejeunea laetevirens* Nees & Mont. – Neotropical, North American, Galápagos Islands. Río Genio, 260 (UCR), 548 (hb. Bernecker).
- Lejeunea* sp. Bahia Iglesias, 633 (hb. Bernecker); Río Genio, 265, 499, 519 (hb. Bernecker).
- Microlejeunea acutifolia* Steph. – Neotropical. Bahia Iglesias, 617 (ULM); Río Genio, 516 (hb. Bernecker), 537 (UCR).
- Microlejeunea bullata* (Taylor) Steph. – Neotropical, Galápagos Islands. Río Genio, 276, 540 (hb. Bernecker); Wafer Bay, 483 (UCR).
- Microlejeunea epiphylla* Bischl. – Neotropical, Galápagos Islands. Iglesias D, 583 (hb. Bernecker), 621 (UCR).
- Lepidolejeunea involuta* (Gottsche) Grolle – Neotropical and Asian. Iglesias E, 606 (hb. Bernecker).
- Lepidolejeunea ornata* (Robins.) R. M. Schust. – Neotropical. Bahia Iglesias, 459 (UCR), 461, 462 (hb. Bernecker), 617 (ULM).
- Leptolejeunea elliptica* (Lehm. & Lindenb.) Schiffn. – Neotropical and Asian, Galápagos Islands, brood branches. Bahia Iglesias, 460, 463 (UCR), 462 (hb. Bernecker); Iglesias A, 697 (UCR); Iglesias D, 582 (hb. Bernecker); Río Genio, 320 (ULM), 636 (UCR).
- Leptolejeunea radicata* (Nees & Mont.) Grolle – Neotropical and African, brood branches. Iglesias A, 554 (UCR), 561 (ULM), 566, 650 (hb. Bernecker).
- Odontolejeunea lunulata* (F. Weber) Schiffn. – Neotropical and African, brood branches. Bahia Iglesias, 458 (ULM), 465 (UCR), 468, 470 (hb. Bernecker), Colnett, 453 (UCR); Iglesias A, 560 (UCR); Iglesias C, 576 (UCR), 578 (hb. Bernecker); Río Genio, 534 (hb. Bernecker).
- Omphalanthus filiformis* (Sw.) Nees – Neotropical, Galápagos Islands. Iglesias E, 282 (hb. Bernecker), 283 (UCR).
- Prionolejeunea* sp. Río Genio, 256, 291, 506 (hb. Bernecker).
- Rectolejeunea berteriana* (Gottsche) A. Evans – Neotropical. Río Genio, 549 (UCR); Wafer Bay, 493 (hb. Bernecker).
- Symbiezidium transversale* (Sw.) Trevis. – Neotropical, Galápagos Islands. Iglesias D, 289 (UCR), 290 (ULM), 589, 590 (hb. Bernecker); Río Genio, 286 (hb. Bernecker).
- Radula flaccida* Lindenb. & Gottsche – Neotropical and African, discoid gemmae. Río Genio, 508 (UCR), 512 (ULM), 523, 527, 528 (hb. Bernecker).
- Musci:
- Crossomitrium patrisiae* (Brid.) C. Müll. – Neotropical, Galápagos Islands, brood bodies. Río Genio, 518 (hb. Bernecker).
- * *Lepidopilum* c.f. *muelleri* (Hampe) Mitt. – Neotropical. Río Genio, 369 (hb. Bernecker); Iglesias A, 370 (UCR); Iglesias E, 371 (ULM).

of the liverworts currently known from Cocos Island. The 45 species belong to four different families and 22 genera. Only two species, *Crossomitrium patrisiae* (Hookeriaceae) and *Lepidopilum* cf. *muelleri* (Calliostaceae) are mosses. The rest belong to the liverworts, of which 42 species are members of the Lejeuneaceae. The Radulaceae are represented only by *Radula flaccida*.

A noteworthy phenomenon on Cocos Island was the frequent occurrence of epiphyllous bryophytes on the underside of the leaves, especially in the mountainous area around Cerro Iglesias, in rather open sites in the elfin forest.

More than half (24) of all epiphyllous bryophyte species are able to produce vegetative propagules (Table 1). Discoid gemmae were found in 17 species

belonging to the genera *Aphanolejeunea*, *Cololejeunea*, *Colura*, *Cyclolejeunea*, *Diplasiolejeunea*, and *Radula*, and brood branches occurred in five species belonging to *Drepanolejeunea*, *Leptolejeunea*, and *Odontolejeunea*. The moss *Crossomitrium patrisiae* exhibits tripartite brood bodies.

Ecogeography. Many species of epiphyllous bryophytes (67%) were present only on one or a few phorophyte plants (Fig. 2). Only a few species, like *Odontolejeunea lunulata* and *Cyclolejeunea convexistipa*, were very common on the island.

Species diversity of epiphyllous bryophytes was significantly different between the investigated sites ($\chi^2 = 62.32$; $df = 10$; $P < 0.0001$). Following prevailing winds from SW to NE and starting at the highest point of the island, the peak of Cerro Iglesias (Iglesias E), species richness was high, decreasing towards the NE (Fig. 3). Species numbers then increased again, and the highest diversity was reached at the valley of Río Genio. Further to the NE, diversity decreased towards Chatham Bay, where no epiphylls were found. At sites where only a few epiphyllous bryophytes occurred, these were mainly species of *Odontolejeunea*, *Cololejeunea*, and *Diplasiolejeunea*.

Epiphyllous bryophytes species composition was investigated for each site, according to their overall

frequency across all sites (Fig. 4), i.e., for each site percentage of species considered rare (occurring at 1–3 sites), common (occurring at 4–8 sites) and frequent (occurring at 9–10 sites) was calculated (see R. Lücking & A. Lücking 1995). All species occurring at Colnett and Presidio Peninsula were common or frequent, belonging mainly to *Odontolejeunea*, *Cololejeunea*, and *Diplasiolejeunea*. The percentage of rare species was highest at Iglesias E and Río Genio, including *Lejeunea laetevirens*, *Radula flaccida*, and *Crossomitrium patrisiae*. The remaining species chiefly belong to *Aphanolejeunea* and *Microlejeunea*, genera in which the smallest species of epiphyllous bryophytes are found.

Species numbers of epiphyllous bryophytes ranged between 0 at Chatham Bay and 32 at Río Genio (Table 2). As expected, the estimated true number of species (Jackknife Estimate \hat{S}) is higher than the number collected. Low CVs were found at Río Genio, Iglesias A and Iglesias C–E, indicating a somewhat more homogenous distribution pattern of epiphyllous bryophytes, i.e., most of the species were present on several different phorophyte plants and few unique species occurred. A higher CV at Wafer Bay, Presidio Peninsula and Iglesias B indicates that many of the epiphyllous species were unique and occurred on only one phorophyte plant.

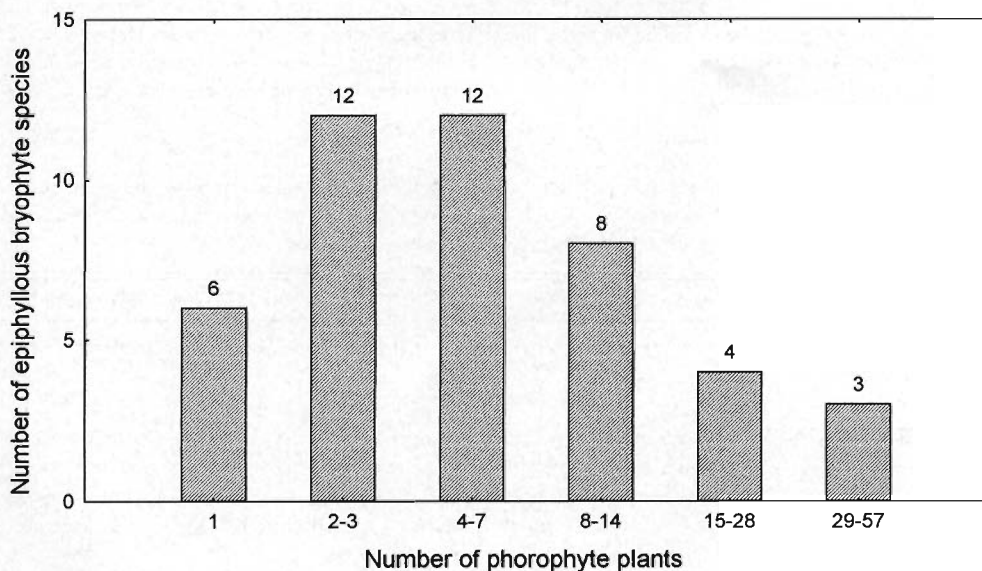


FIG. 2. Frequency distribution of epiphyllous bryophytes based on the number of phorophyte plants on which each species was present (total of 57 phorophytes).

Distribution of epiphyllous bryophytes among the different sites, and their abundance (presence on the phorophyte plants) is shown in Table 3. Only the commonest epiphyllous bryophytes (i.e., present on more than 10% of all phorophyte plants) were taken into consideration. *Diplasiolejeunea inermis* was present at all sites. Some species, mainly of the genera *Cololejeunea*, *Diplasiolejeunea*, and *Radula*, occurred only at sites in the northeastern part of the island, whereas species of the genera *Cyclolejeunea* and *Drepanolejeunea* were present principally in the southwestern part. Nearly all of the species were present at Río Genio or Iglesias A. *Cyclolejeunea accedens* occurred only at Iglesias E, but there it was abundant and present on eight of the nine phorophyte plants investigated. *Cololejeunea cardiocarpa* occurred mainly at Wafer Bay.

The cluster analysis of the sites based on epiphyllous bryophytes species composition revealed two main groups (Fig. 5). Group I is further divided into two sections: Section 1 (Wafer Bay, Iglesias A, Río Genio, Iglesias Bay) represents the lower level and coastal regions of the island. Section 2 (Iglesias E, Iglesias D) corresponds to the mountainous regions characterized by an elfin forest. Group II (Iglesias B and C, Colnett Peninsula) represents the transitional area between the lowland and the mountains and the drier parts of the island, with low epiphyllous species diversity. Presidio Peninsula is isolated and not included in any group.

No correlations could be found between the diversity of epiphyllous bryophytes and that of the phorophytes.

DISCUSSION

Phytogeography. The epiphyllous bryophytes of Cocos Island can be assigned to five geographical distribution types according to their distribution (Fig. 6). All species are known to be present at other sites in the Neotropics and 68% of them are widespread. Cocos Island shares about 30% of its epiphyllous bryophyte flora with the Galápagos Islands. A similar pattern is found in comparing the distribution of epiphyllous bryophytes with those growing on humus or bark, or with the bryophytes reported from Galápagos Islands (Gradstein & Weber 1982, Dauphin 1995). Compared with the Galápagos Islands, differences exist mainly in endemism: on Cocos Island only 3% of the species growing on humus or bark and none of the epiphyllous bryophytes are endemic, whereas on the Galápagos Islands 11% of the reported bryophytes are endemic. Likewise in vascular plants, endemism is much higher on the Galápagos Islands than on Cocos Island (Stewart 1912, Lawesson *et al.* 1987, Montoya 1990, Fournier pers. comm). This difference in degree of endemism may be due to the fact that the Galápagos Islands are geologically older (4 million years) than Cocos Island (2 million years) (Bailey 1976, Bellon *et al.* 1983). Endemism also increases with the degree of isolation (Fosberg 1970) or with dryness of climate, characteristics of the Galápagos Islands (Colinvaux 1972, Gradstein & Weber 1982).

Since Cocos Island is an oceanic island which was never connected to the continent (Stewart 1912, Hertlein 1963, Gómez 1986, Montoya 1990), colonization has taken place by means of wind, sea cur-

TABLE 2. Jackknife Estimate of species richness. S: total number of species present on n phorophytes; n = total number of phorophytes (sampling quadrates); \hat{S} : Jackknife Estimate of species richness; SD: standard deviation of the Jackknife Estimate; CV: coefficient of variation.

Locality	S	n	\hat{S}	SD	CV (= SD / \hat{S})
Chatham Bay	0	0	0	0	0
Colnett Peninsula	4	1	4.00	0	0
Presidio Peninsula	6	3	9.33	3.40	0.26
Wafer Bay	16	7	23.71	5.02	0.21
Río Genio	32	10	42.80	6.41	0.15
Cerro Iglesias A	19	6	27.33	4.58	0.17
Cerro Iglesias B	10	4	13.75	2.84	0.21
Cerro Iglesias C	9	5	13.80	1.96	0.14
Cerro Iglesias D	14	5	18.80	2.33	0.12
Cerro Iglesias E	22	9	30.75	5.43	0.18
Iglesias Bay	21	7	29.54	5.83	0.20

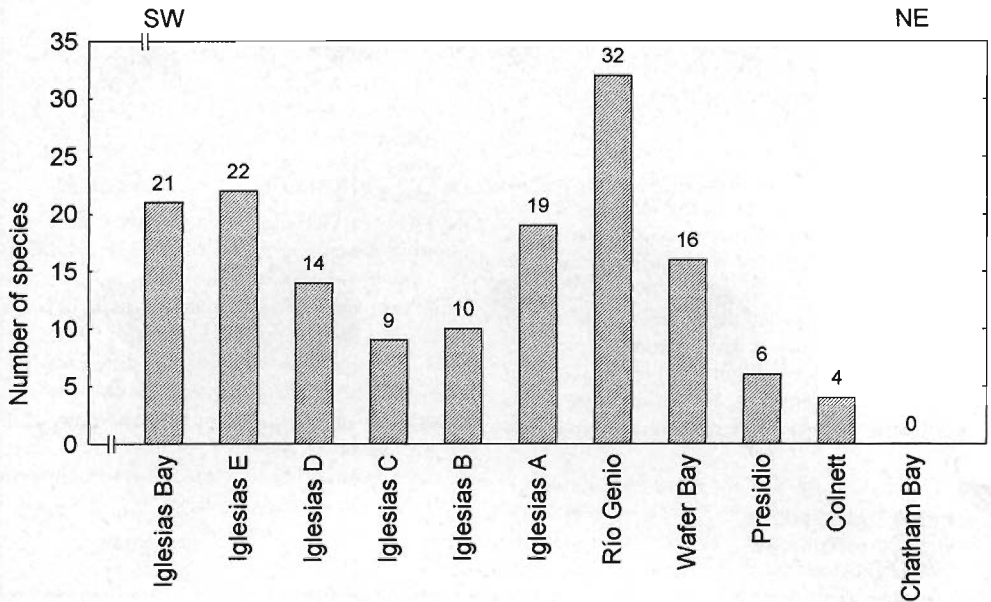


FIG. 3. Species numbers at the investigated sites, arranged from southwest (SW) to northeast (NE). Species diversity was significantly different between the sites ($\chi^2 = 62.32$; $df = 10$; $P < 0.0001$).

rents, migratory birds or anthropogenic introduction (van Steenis 1964, Fosberg 1970). Spores and vegetative propagules of epiphyllous bryophytes have the potential to be transported by air currents over moderately long distances since they are usually very small (van Zanten & Pócs 1981). Species from Central America and northern South America seem to have the best chance of reaching Cocos Island by westward ocean and wind currents. And so it is no surprise that the phytogeographical affinities of the epiphyllous bryophyte flora are mainly with the Neotropics, nearly all species occurring in Central or northern South America.

Floristics and ecogeography. The species richness of epiphyllous bryophytes on Cocos Island was half that of a site studied on mainland Costa Rica (A. Lücking 1995). Similar investigations revealed 52 species in Colombia (Winkler 1970), 46 species in Sabah, northern Borneo (Mizutani 1966), and 47 species in French Guiana (Montfoort & Ek 1990). For the French Antilles 77 species of epiphyllous bryophytes from 143 investigated sites are reported (Jovet-Ast 1949). Taking into consideration that the sites on Cocos Island were much more diverse in altitude and

vegetation structure (from open littoral vegetation to upper montane forest) than the sites where similar investigations were carried out, species numbers could be expected to be much higher. However, Cocos Island follows the general phenomenon that islands have fewer species of plants and animals than do comparable continental areas (Fosberg 1970, Wilson 1996).

The high species diversity but low density of individuals among epiphyllous bryophytes on Cocos Island is quite typical for the structure of tropical rainforests in general (Reichholf 1991). Some of the epiphyllous taxa occur not only on living leaves but also on bark (*Aphanolejeunea sicaefolia*, *Ceratolejeunea rubiginosa*, *Cheilolejeunea rigidula*, *Cyclolejeunea convexistipa*, *C. peruviana*, *Cystolejeunea lineata*, *Lejeunea (Microlejeunea) bullata*, *Lepidolejeunea ornata*, *Omphalanthus filiformis*, *Rectolejeunea berteriana*, *Symbiezidium transversale*, *Crossomitrium patrisiae*) or humus (*Drepanolejeunea crucianella*) (Dauphin 1995, A. Lücking 1995). *Omphalanthus filiformis* or *Symbiezidium transversale* are more frequently found growing on bark, at least at other sites in the Neotropics (A. Lücking 1995), while species of *Aphanolejeunea* are

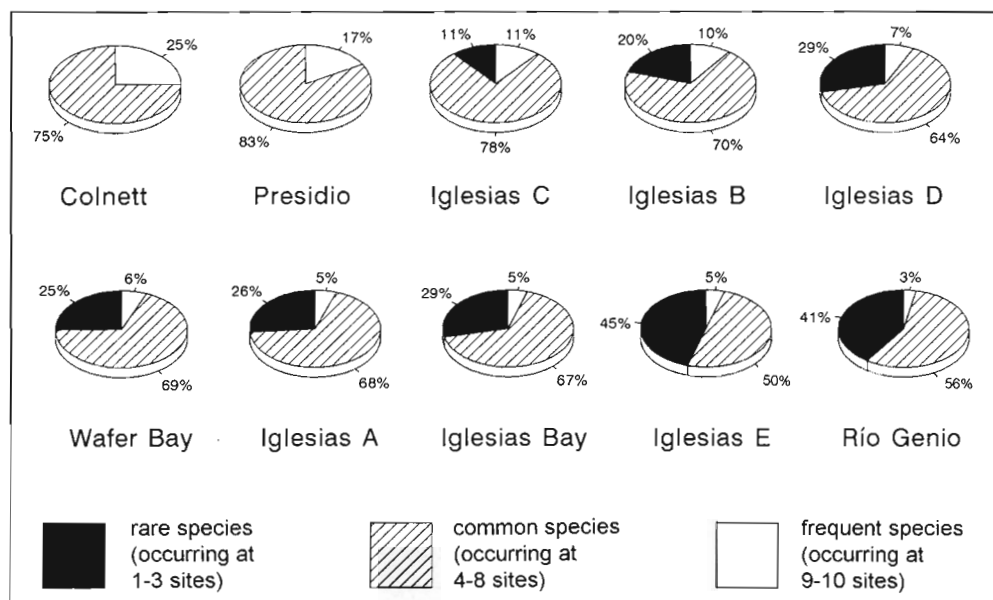


FIG. 4. Percentage of species occurring at 1-3, 4-8 or 9-10 sites for each of the examined sites. Chatham Bay is not considered because of the absence of epiphyllous bryophytes.

known almost exclusively from living leaves (Pócs 1984). Species of *Cyclolejeunea* are often very dominant on living leaves but also grow well on twigs and small branches (Cornelissen & ter Steege 1989, Montfoort & Ek 1990).

The occurrence of epiphyllous bryophytes on the undersides of the leaves is known from other sites, but only when the leaves are turned upside-down accidentally (Bien 1982). Hypophyllous bryophytes on Cocos Island are found frequently in the mountainous area around Cerro Iglesias, which is known to receive a considerable amount of misty precipitation (Montoya 1990). This water source, together with fairly good light conditions in the more open vegetation, may be the reason for the hypophyllous growth of these species.

The most important factor affecting the distribution pattern of the species between the different sites seems to be microclimatic conditions, especially the availability of water. Although Cocos Island is very small and rainfall amounts to 7000 mm per year (Herrera 1985, Montoya 1990), the southwestern part probably receives more precipitation than the northeastern part, because for most of the year prevailing winds come from the southwest (Montoya

1990). This assumption was strengthened by an observation made during my stay on the island, when heavy rain fell in the region around Cerro Iglesias in the southwest, whereas in the northeast the area from Wafer Bay to Chatham Bay remained dry. Unfortunately, climatic measurements from different sites on the island are not available.

The absence of epiphyllous bryophytes at Chatham Bay might be due to its leeward position and dryness. Differences in precipitation rates may have the strongest effect in the drier season between January and March (Herrera 1985), most of all when the warm ocean current "El Niño" causes drastic changes in the climate every 7-8 years (Montoya 1990, Weber & Beck 1985). These changes in temperature and precipitation rates may cause serious disturbances in the bryophyte vegetation and diminish species diversity.

At Colnett and Presidio Peninsulas only a few species of epiphyllous bryophytes were found. They were common or frequent considering their overall occurrence across all sites, but at Colnett or Presidio Peninsula most of them were only present on one phorophyte plant, although the surrounding vegetation is very homogenous. They may be restricted to

one plant because the appropriate climatic conditions are only present there. Some of them, like *Cololejeunea marginata* and *Diplasiolejeunea inermis*, are adapted to drier habitats and grow closely appressed to the substrate, so that water can be retained under the whole surface of the plant. Low population density and clustering of individuals indicate that the epiphyllous bryophyte flora at Colnett and Presidio Peninsulas is not very well developed.

Very humid conditions around Cerro Iglesias (Iglesias E, D) are indicated by the presence of an elfin forest and some species of epiphyllous bryophytes that are characteristic of humid sites (A. Lücking 1995). One of them, *Cyclolejeunea accedens*, was present only at Iglesias E, but was very common at this site. It is well adapted by the presence of papillae on the dorsal surface of the lateral leaf cells that enhance transpiration and maintain gas exchange in moist habitats (Proctor 1979, Bernecker-Lücking 1998, A. Lücking 1995). I made the interesting observation that the dorsal cell walls of the lateral leaves of *Cyclolejeunea convexistipa* have strongly bulging sides, a modification not previously described and which also appears to be an adaptation to humidity. Distinctly dentate leaf margins are also useful in enhancing transpiration, and are characteristic of *Drepanolejeunea crucianella*, *Odontolejeunea lunulata*, and all species of *Cyclolejeunea*.

Although located in the northeastern part of Cocos Island, humidity in the valley of Río Genio is

high, due to evaporation from the river and several waterfalls. Iglesias E and Río Genio are characterized by the highest species numbers and the presence of many epiphylls that are rare on Cocos Island. Favorable climatic conditions at both sites might be the reason for this well-developed flora. More so than other plants, epiphyllous bryophytes depend on regular rainfall or high humidity in the atmosphere, because water cannot be stored on the leaf surface of the phorophyte. *Symbiezidium transversale*, for example, is common on bark but grows also on living leaves if enough humidity is available. *Lejeunea laetevirens*, *Radula flaccida*, *Crossomitrium patrisiae*, and species of the genera *Aphanolejeunea* and *Microlejeunea* grow closely appressed to the substrate or tend to be very small. Therefore, they might be easily overgrown and displaced by large and fast growing generalists. They may be only well represented if their competitors are inhibited (A. Lücking 1995). The lack of water in the dry season may inhibit or damage dominant taxa, whereas the remaining humidity allows the survival of most species, leading to the maintenance of a high species diversity.

The high diversity of epiphyllous bryophytes at Río Genio might also be explained by the fact that many species might have been introduced to Wafer Bay with agricultural plants like *Coffea arabica*, *Mangifera indica* or *Citrus* spp. about 100 years ago. As in foliicolous lichens (R. Lücking 1992, R. Lücking & A. Lücking 1995), there are some epiphyllous

TABLE 3. Distribution of epiphyllous bryophyte species across all sites, taking into consideration only species found on 7 or more phorophyte plants (more than 10%). (○) species present on less than 50% of the phorophytes at the site; (●) species present on 50% or more of the phorophytes at the site. (–) species not present at the site. Chatham Bay is not considered because of the absence of epiphyllous bryophytes.

Taxa	Iglesias Bay	Iglesias E	Iglesias D	Iglesias C	Iglesias B	Iglesias A	Río Genio	Wafer Bay	Presidio	Colnett
<i>Cololejeunea cardiocarpa</i>	–	–	–	–	–	○	–	●	–	–
<i>Cololejeunea marginata</i>	○	–	–	–	●	●	○	●	●	●
<i>Cyclolejeunea accedens</i>	–	●	–	–	–	–	–	–	–	–
<i>Cyclolejeunea convexistipa</i>	●	●	●	○	●	○	–	–	–	–
<i>Diplasiolejeunea inermis</i>	●	●	●	●	●	●	–	○	○	●
<i>Diplasiolejeunea pellucida</i>	–	–	–	–	–	●	–	○	○	–
<i>Drepanolejeunea crucianella</i>	●	●	●	–	–	–	–	–	–	–
<i>Leptolejeunea elliptica</i>	●	–	○	–	–	●	–	○	–	–
<i>Leptolejeunea radicata</i>	○	–	○	–	–	●	○	–	–	–
<i>Odontolejeunea lunulata</i>	●	–	●	●	●	●	●	○	–	●
<i>Radula flaccida</i>	–	–	–	–	–	○	–	○	–	–

bryophytes that are regularly found on living leaves of agricultural plants. They are adapted to more open and drier habitats, like species of the genus *Leptolejeunea*, *Colura* or *Radula flaccida* (Pócs 1978, Gradstein & Weber 1982). They may have dispersed to the adjacent valley of Río Genio where they were able to survive even in the very dry periods caused by "El Niño".

The distribution of epiphyllous bryophytes among the different sites also seems to be related to vegetation diversity. Rare species are absent in the northeastern plateau of Presidio and Colnett Peninsulas, or are represented to a small degree at Cerro Iglesias B and C (Fig. 4). At all these sites I observed a similar, more homogenous vegetation. In contrast, a high percentage of rare species of epiphyllous bryophytes are present if the surrounding vegetation is more diverse, as is the case in the elfin forest of the upper mountain region of Cerro Iglesias E and D, and the lowland forest developed at Río Genio and at Iglesias Bay. The groups revealed by cluster analysis reflect these different vegetation types and distribution of rare species, although no correlations could be

found between epiphyllous bryophytes and phorophytes in the data analysis, and also reflect the differences in climatic conditions already discussed.

The influence of the phorophyte species on the epiphyllous flora growing on their leaves seems to depend mainly on the structure of the leaf surface, especially the presence or absence of hairs (R. Lücking 1994, A. Lücking 1995). Large species of epiphyllous bryophytes, for example, do not find enough space to grow between closely standing hairs. But those leaves might be colonized by small species, which might be overgrown and therefore displaced by larger species on smooth leaves. The effect of chemical substances released by the phorophytes through excretion or leaching has been discussed. The remarkably good colonization of *Citrus* trees by epiphylls has often been noticed, but to date results have been inconclusive (Pócs 1982).

Epiphyllous bryophytes and foliicolous lichens. When numbers of species of epiphyllous bryophytes and foliicolous lichens are compared (R. Lücking & A. Lücking 1995), it is evident that a 1:2 ratio exists not

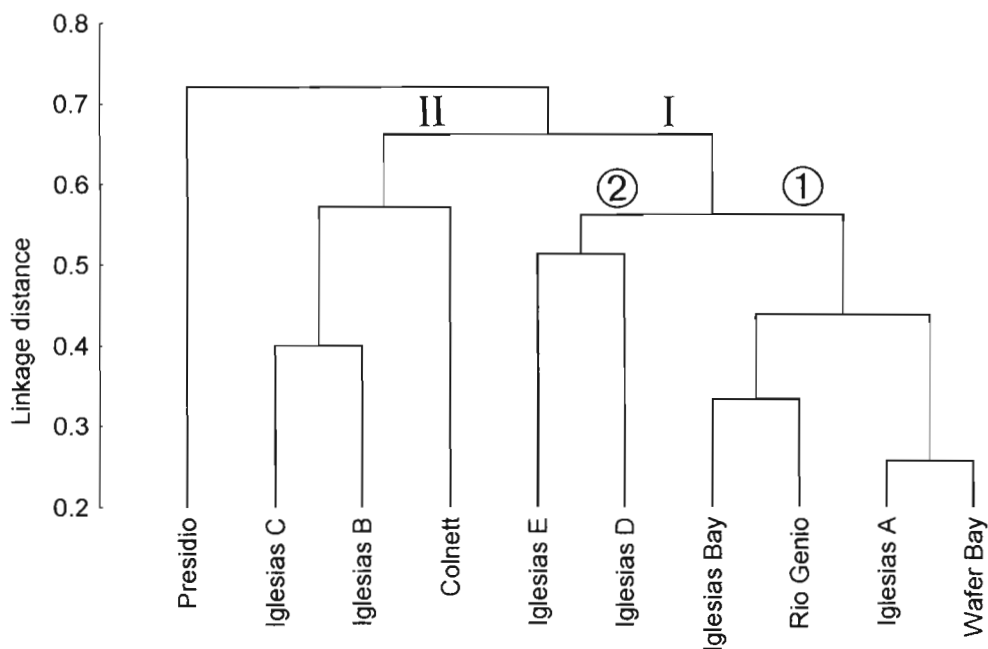


FIG. 5. Cluster analysis of the sites based on their epiphyllous bryophyte species composition. Group I is divided into 2 sections: section ① represents the lower level and coastal region, section ② the mountains. Group II corresponds to the transitional elevations and drier parts of the island. Chatham Bay is not considered because of the absence of epiphyllous bryophytes.

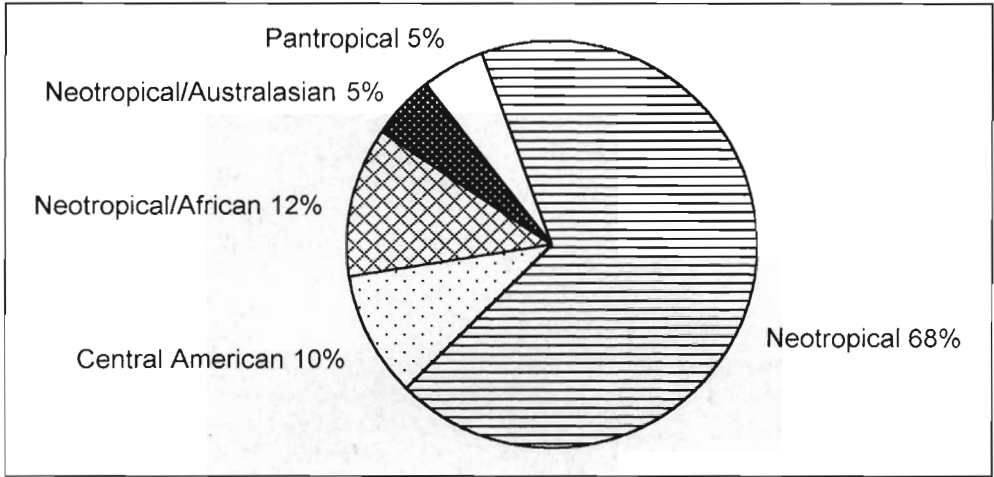


FIG. 6. Percentages of different geographical distribution types present in the epiphyllous bryophyte species on Cocos Island. Neotropical: widespread Neotropical; Central: Central American, Caribbean or northern South American; Neotropical/African: Neotropical and African; Neotropical/Australasian: Neotropical and Australasian; Pantropical: widespread pantropical.

only on Cocos Island but also at a site investigated on mainland Costa Rica (A. Lücking 1995). In both groups, many of the species found on the island were rare, with only a few individuals of each species present. Since the foliicolous lichen flora was much more diverse, rare species reach higher percentages at all sites.

Comparing the distribution of epiphyllous bryophytes and foliicolous lichens (R. Lücking & A. Lücking 1995), a similar pattern of species richness was observed in the northeastern part of the island: Chartham Bay without foliicolous lichens and Río Genio with the highest diversity. Differences existed mainly in species number at sites in the southwest of the island. In foliicolous lichens, species numbers decreased with altitude and increasing humidity, a general phenomenon in communities of foliicolous lichens (Santesson 1952, R. Lücking 1995), whereas diversity in epiphyllous bryophytes increased. Competition between the two groups may play an important role in this phenomenon. Increasing humidity favors epiphyllous bryophytes, which displace foliicolous lichens simply by overgrowing. The cluster analysis of the sites based on species composition in foliicolous lichens revealed two groups, as found in epiphyllous bryophytes and was already discussed (see R. Lücking & A. Lücking 1995).

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