

BRYOGEOGRAPHY OF THE GALAPAGOS ISLANDS¹

S. R. GRADSTEIN² AND WILLIAM A. WEBER³

RESUMEN

De las Islas Galápagos se conoce más de 200 especies de briófitas (el número total de los musgos y de las hepáticas es de mas o menos igual). Más que 2/3 partes de las especies ocurren en la selva y matorrales perennifolias y húmedas limitadas a las zonas altas de algunas islas.

Una proporción elevada (65-70%) de la brioflora trata de especies de una distribución amplia y neotropical o ampliamente tropical, que probablemente han llegado con los vientos predominantes orientales del continente sudamericano. Generalmente las briófitas de las Islas Galápagos tienen una dispersión excelente, al contrario de otros grupos de organismos.

Mas o menos 85% de las hepáticas produce esporos y/o gemmae y aproximadamente 40% de las especies son bisexuales. Además es interesante anotar que taxa sin diásporas están limitados hacia una sola isla, y que taxa con formación de diásporas tienen una distribución más amplia según las condiciones ecológicas favorables. Una proporción bastante elevada (20%) de los musgos pertenece al elemento "oceánico-Caribe" probablemente llegado con los vientos alisios desde las costas de Centro-América o directamente de las Antillas vía el Istmo de Panamá

Este grupo de especies se encuentra en las Islas Galápagos en alturas más bajas, con preferencia cerca de la costa. Unas pocas especies templadas y disyuntas están presentes en las pampas frías y secas de Isabela arriba de 1200 m. Además taxa cosmopolitos y ciertos taxa endémicos son común en las pampas.

La proporción de los taxa endémicos es más elevada entre las hepáticas (16%) que entre los musgos (6%). Taxa endémicos ocurren con preferencia en las regiones abiertas y secas en las Islas Galápagos, probablemente debido a que este medio ambiente para selección natural y evolución existía ya hace más tiempo, como es corroborado por evidencia palaeobotánica.

Se trata de caracterizar y comparar la brioflora de Galápagos, aunque las listas de recopilación para briofloras regionales del trópico hacen falta en una forma tremenda. En comparación con la brioflora del continente sudamericano la de las Islas Galápagos es un poco pobre en especies; faltan marcadamente taxa de la selva húmeda tropical y de selva nublada.

La proporción bastante elevada de hepáticas talosas del orden Marchantiales caracteriza la brioflora de las Islas Galápagos como mas o menos mesofítica y subtropical, a pesar de la presencia elevada de Lejeuneaceae.

INTRODUCTION

In contrast to vascular plants, which were comprehensively treated by Wiggins & Porter (1971), little has been published on the bryophytes of the Galapagos Islands. Weber (1966) listed 40 mosses and 71 hepatics known up to the time of the Galapagos International Scientific Project in 1964, supposedly representing "only a small fraction of the flora", since bryophyte collecting up to then had been entirely the incidental gatherings of non-specialists. Weber (1976) added to this list as the result of his 1964, 1971 and 1972 collections. Efforts toward investigating the Galapagos bryo-

¹ Contribution No. 292 of the Charles Darwin Foundation.

² Institute of Systematic Botany, Heidelberglaan 2, Utrecht, Netherlands.

³ University of Colorado Museum, Campus Box 218, Boulder, Co 80309, U.S.A.

phytic flora in more detail were made during a three-month exploration by the authors, supported by grants from the National Geographic Society and the Netherlands Foundation for the Advancement of Tropical Research (WOTRO) in 1976, during which collections were made on all the main islands. In addition, important additions were made by Dr. Ole Hamann during the 1970's. Several hundred collections were made by Dr. Henk H. Van der Werff on Santa Cruz and Isabela in the framework of vegetation studies (Werff 1978). Tui De Roy Moóre and Uno Eliasson, among others, made collections of several critical species at our request. These collections are the basis for the bryogeographical analysis presented herein.

Identification of the materials has been carried out with the help of several specialists whose help is gratefully acknowledged: in the Hepaticae, Helène Bischler (*Plagiochasma*, *Sauteria*), Ella Campbell (*Marchantia*, *Fossombronia*), Riclef Grolle (*Cheilolejeunea*, *Prionolejeunea*, *Tylimanthus*), Jiro Hasegawa (*Anthocerotae*), Hiroshi Inoue (*Plagiochila*), Suzanne Jovet-Ast (*Riccia*), Yukinobu Kuwahara (*Metzgeria*), Maurice Onraedt (*Taxilejeunea*) and Jiri Vána (*Neesioscyphus*); in the mosses, Marshall Crosby (Hookeriaceae), Howard Crum, Dana Griffin III, and William C. Steere (general), Richard Zander (Pottiaceae), Jan-Peter Frahm and Harrie Sipman (*Campylopus*), Harrie Sipman and Ronald Pursell (*Fissidens*), Richard E. Andrus (*Sphagnum*), and William Buck (Fabroniaceae).

The appendix lists 102 species of named liverworts and 102 species of mosses for the islands. The total number of species should rise to over 225, however, since for several sterile mosses (10 spp.), some Lejeuneaceae (6 spp.), *Cephaloziella* (3 spp.) and sterile *Symphogyna* (?), identifications are still lacking or uncertain.

The main questions that we would like to pose in this paper are:

1. What is the composition and origin of the bryophyte flora of the Galapagos Islands?
2. How does the flora of the islands compare with that of other tropical regions or islands?

Before developing these topics we should give a brief impression of Galapagos physiography, climate and vegetation as they bear on the occurrence of bryophytes. The reader is advised that discussions concerning Hepaticae represent the observations of Gradstein, those regarding the mosses the observations of Weber.

PHYSIOGRAPHY, CLIMATE AND VEGETATION

The Galapagos Islands are a group of very young volcanic islands along the Equator in the eastern Pacific Ocean, about 1,000 km west of the South American mainland (Fig. 1). Vulcanologists estimate the maximum age at about three million years (Bailey 1976). Although the presence of land bridges has been suggested in the past, there seems to be no geological evidence that the islands were ever connected to the mainland. It may thus be safely concluded that the archipelago is truly of oceanic origin (thalassogenic) and, in view of their Late Pliocene age, the flora and fauna should be recent colonists. There are some 45 islands covering about 7,900 km² in toto but

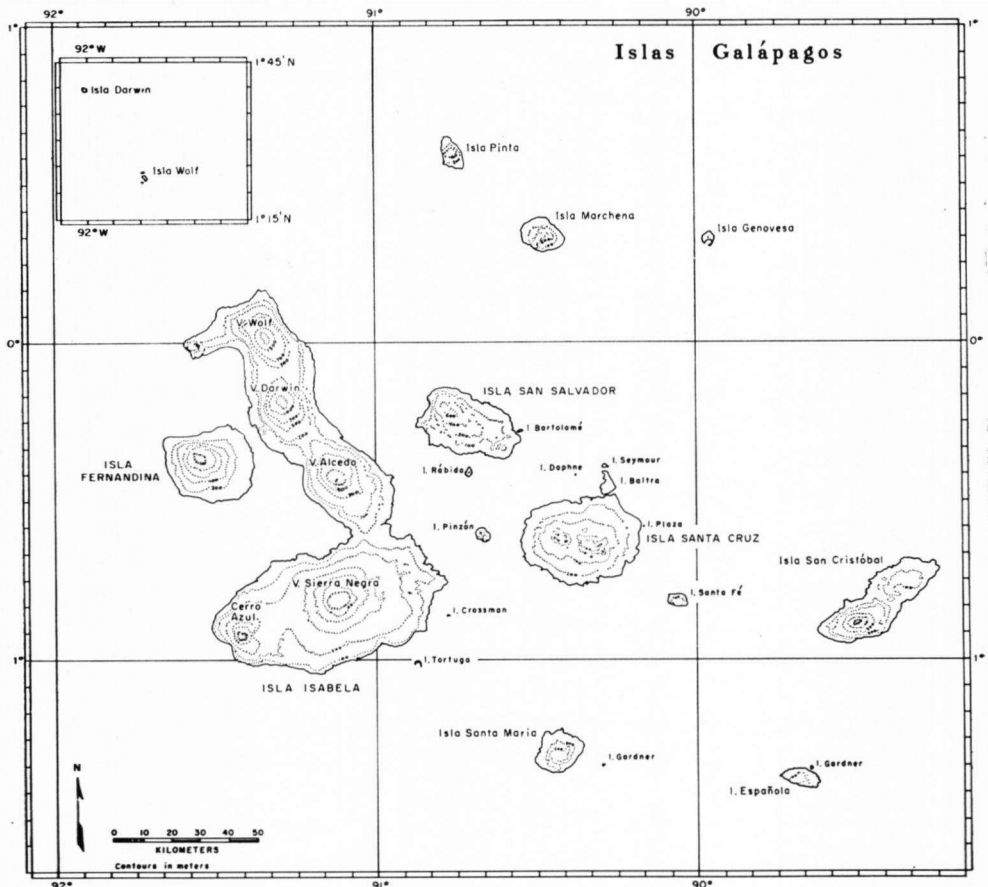


FIG. 1. General map of the Galapagos Islands.

most of these are very small and low; a large portion of their total surface is extremely dry and intensely insolated, with sparse vegetation. Eight islands reach above 400 m (maximum altitude on Isabela 1,700 m) and support a vegetation verdant enough to harbor a diversified bryophyte flora: Fernandina, Isabela, Pinta, Pinzon (Duncan), Santa Cruz, Santa Maria (Floreana), San Cristobal and San Salvador (James).

Although located along the Equator, the islands are in the centre of the so-called "Pacific Dry Zone" characterized by a climate much dryer than in other tropical regions (Palmer & Pyle 1966). Two seasons are recognized in the Galapagos: the cool season (July–December) and the warm season (January–June). During the cool season the cold Humboldt current from the south generates low air temperatures, "garua" (more or less continuous drizzle) and fog in the uplands; temperatures at sea level go down to ca. 19°C. During the warm season, the arrival of warm surface waters from the north (the "El Nino" current) causes air temperature at sea level to rise maximally to 29°C. Instead of garua, an irregular rainfall pattern of showers

TABLE 1. Total rainfall (in mm) at different altitudes on the southern slope of Santa Cruz during two subsequent years (after Van der Werff, 1979).

Location Altitude Vegetation Zone	C.D.R.S. 6 m I	Caseta 200 m III a	Devine's farm 350 m III a	Media Luna 620 m III b
1969	470	1586	1902	2656
1970	84	402	425	1154

alternating with periods of drought is characteristic for the warm season. With increasing altitude, air temperatures go down whereas precipitation increases. Total annual precipitation varies (Table 1) but does not seem to exceed 3000 mm in the uplands during the wettest years. It should be noted, however, that these measurements do not take into account the effect of fog condensation on the vegetation. According to van der Werff (1978), condensation may, in the mesic highlands, locally account for up to *five hundred times* the actually measured monthly rainfall and causes permanent wetness of the vegetation. For the development of bryophyte vegetation this phenomenon is of great significance; in the uplands crustose epiphytic lichens are almost completely excluded by bryophytes, and even large foliose lichens (*Sticta* and *Pseudocyphellaria*) are relatively uncommon, while the slender fruticose *Ramalina*, *Pseudevernia* and *Usnea* compete successfully only on branches relatively bare of mosses for whatever reasons. Too few measurements are available, however, for precise ecological correlations. An interesting climatological phenomenon is the presence on Isabela (the only island reaching higher than 1000 m) of a so-called "inversion" layer, above which rainfall decreases sharply, causing the development of cool and

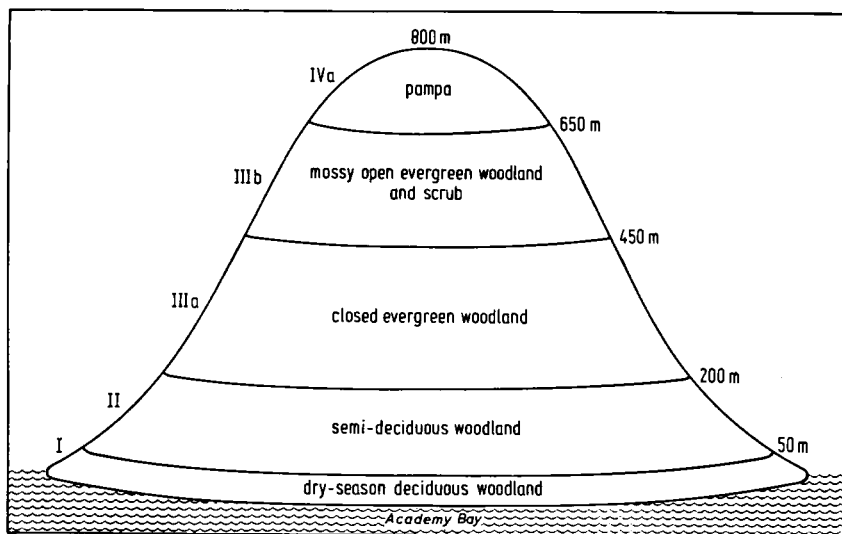


FIG. 2. Vegetation zones on the southern slopes of Santa Cruz (modified after Bowman, 1963).

dry summit zones. This is where some disjunct temperate bryophytes (and lichens) occur.

At the present time, winds in Galapagos are strongest during the cool season when they blow from southeast directions (Peru – Ecuador). During the warm season winds are east to northeast (Ecuador – Colombia – Panama) and less forceful. The direction of the prevailing winds is correlated with the neotropical character of the flora. In general, winds are strongest on the southern slopes of the islands, which also receive more rain than the northern (leeward) slopes. It is necessary, however, to remember that wind patterns may not have been the same during the relevant past, when original bryophyte colonists reached the islands.

In correlation with precipitation and altitude several vegetation zones can be distinguished (Fig. 2), which probably are most strongly diversified on the southern slope of Santa Cruz (a gently and evenly rising vegetated volcano bathed by southerly trade winds), from where they were described by several authors (cf. Bowman 1963, Wiggins & Porter, 1971, Hamann 1979, Van der Werff 1979).

ZONE		ALTITUDE ON SANTA CRUZ Southern slope
I	Dry-season woodland zone ("Arid Zone")	10–50 m
II	Semi-deciduous woodland zone ("Transition Zone")	50–200 m
III	Evergreen woodland zone, to be subdivided into	
	a) Closed evergreen forest ("Scalesia Zone")	200–450 m
	b) Mossy, open evergreen forest ("Brown Zone") or mossy evergreen scrub ("Miconia Zone")	450–650 m
IV	Non-wooded summit pampa ("Fern-sedge Zone") to be subdivided into	
	a) mesic evergreen pampa, below inversion layer	650–800 m
	b) dry pampa, above inversion layer	lacking on Santa Cruz, present on Isabela above 1100 m

Different bryophyte assemblages are to be found in the various altitudinal zones (Fig. 3; appendix). The occurrence of bryophyte species as well as different bryogeographical elements in the vegetation zones is discussed below.

BRYOPHYTE DISTRIBUTION IN GALAPAGOS: HABITATS

A brief description of bryophyte occurrence along the altitudinal gradient on the south slope of Santa Cruz was provided by Weber (1966). Some aspects of inter-island distributions and special ecological correlations were discussed by Weber et al. (1977) and Gradstein (1979). Main features are given here.

As might be expected, species richness (Fig. 3) is highest in the evergreen zones with an optimum in the mossy upper woodlands and scrub (67 spp. of liverworts and 66 spp. of mosses). Many bryophytes of the pampa could also be added, since a large part of this grass-sedge-fern area is considered to be a formerly forested fire disclimax. The mossy woodland zone was previously called "Brown Zone" because of the luxuriant brownish epiphyte vegetation, dominated by pendulous *Frullania* spp. of the sect. *Meteoriopsis* (incl. *F. aculeata*, *F. atrata*, *F. mathanii*), and *F. bra-*

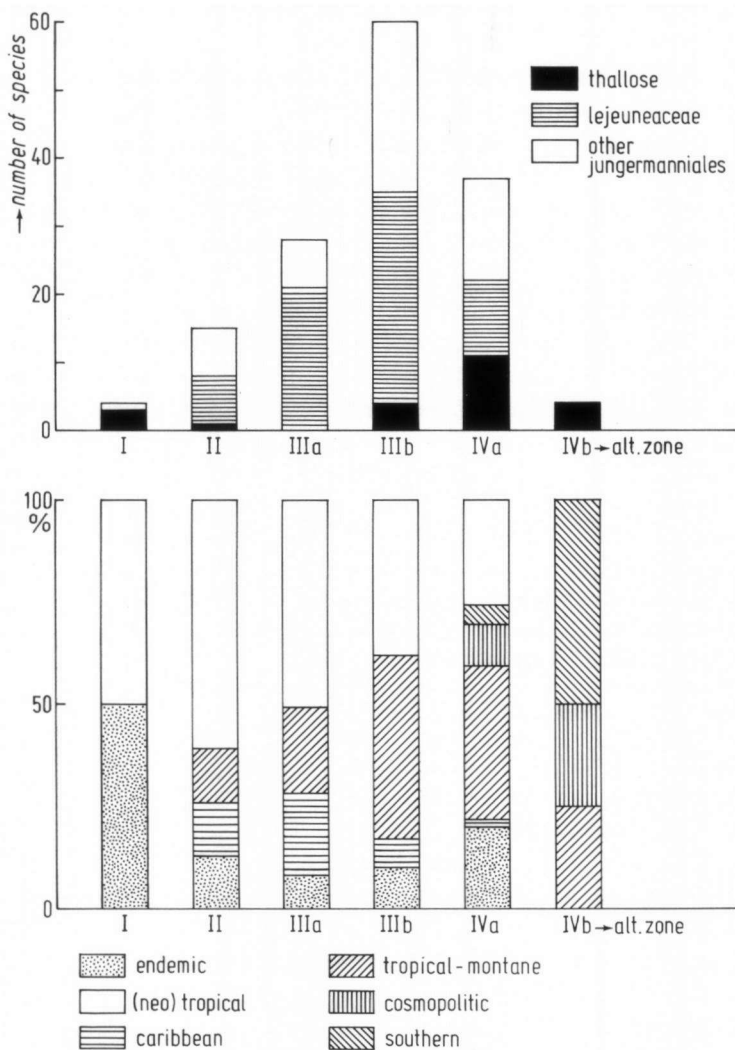


FIG. 3. Species richness and distribution of geographic elements along the altitudinal gradient in the Galapagos Islands, as exemplified by the liverworts.

siliensis, which grows in extensive mats or balls, as well as pendulous mosses of the genus *Squamidium*, and the foliose lichen *Sticta weigelii*. Lejeuneaceae, which account for over a third of the total liverwort flora, are particularly well represented here (Fig. 3).

Thallose liverworts (Metzgeriales, Marchantiales and Anthocerotae) are well-represented on Galapagos (20% of the liverwort flora), which, for Marchantiales, seems to reflect the relatively dry climate. Their optimum is in the drier subtropical and Mediterranean regions (Jovet-Ast et al. 1976). Thallose species are usually

terrestrial, and in contrast to the foliose Jungermanniales, inhabit mainly the open, non-wooded regions (Zones I and IV). Most of them occur on saturated, packed bare soil in the pampa, but some species of *Riccia* occur in the otherwise bryophytically poor Arid Lowland Zone.

Bryophytes are practically absent on the very hot and dry rocky coastal lowland. Only where rocks present prominent vertical surfaces to the moist trade winds and provide some protection from the sun (for example, the steep barranco on Santa Cruz a few hundred yards from the sea) do small colonies of *Campylopus galapagensis*, *Erpodium domingense*, and *Fissidens* share such sites with xerophytic ferns. Mosses first appear in some quantity in Zone II in raised lava hummocks, an indication that the horizontal lava pavement still provides too little protection from desiccation. Here the weedy, pantropical, xerophytic *Frullania ericoides*, the only foliose liverwort entering the Arid Zone woodland, occurs on rocks and on the trunks of smooth-barked trees.

Ground mosses increase with altitude in the Transition zone, particularly species of Pottiaceae such as *Hyophila microcarpa* and *H. involuta*, *Hymenostomum breutelii*, *Tortella humilis*, *Trichostomum jamaicense* and *Racopilum tomentosum*. Soon, leaning tree-trunks are covered, near the ground, with mats of *Groutiella mucronifolia* and *Brachymerium systylium*, and the border of the moist zone is signalled by the appearance of large mats of *Frullania brasiliensis* on the spreading branches of large trees, and the ubiquitous *Zelometeorium patulum* and *Squamidium caroli* drape themselves over shrubby, tree branches, and fences.

The moist Evergreen woodland zone has already been mentioned as the richest for bryophytes. Because of the destruction of much of the original *Scalesia* forest (itself a rich habitat) and its replacement by extensively introduced exotic trees and cultivars, this zone probably will continue to yield new discoveries of bryophytes and possibly some of them will have been accidentally imported in modern times with animals, fowl, provisions, shoes and pants-cuffs, just as have so many phanerogams. This area is rich in all forms of cryptogams and has not been sufficiently explored.

The closed evergreen forest more or less abruptly yields, on Santa Cruz at least, to the mossy evergreen scrub (*Miconia* zone) which, because of its somewhat more open nature and abundance of small exposed twigs, harbours a number of interesting hepatics, such as *Metzgeria grandiflora*, *Dendroceros crispus*, *Colura tenuicornis* and ascending mosses such as *Daltonia lindigiana* and *D. longifolia*, some of which are extremely scattered and rare in their occurrence.

In the mesic pampa, which on Santa Cruz has been burned (ca. 1935, according to residents) the wet pot-holes, packed ground of trails, seasonal streams, occasional stands of shrubs and barren volcanic cones and plugs provide many rich and diversified habitats for bryophytes, particularly ground species (*Campylopus*, *Funaria*, *Ceratodon*), thalloid liverworts and semi-aquatic forms (*Sphagnum*, *Isopterygium*). On southern Isabela *Breutelia tomentosa*, *Entosthodon bonplandii*, *Anoetangium aestivum* and *Thuidium recognitum* have their unique stands on the islands in relatively wet pampa where persistent cloud veils may play a part.

The very few permanent springs scattered over the islands in various zones support some of the very "special" mosses, which occur practically nowhere else, and often in only one spring on a single island. *Cyclodictyon albicans*, *Crossomitrium orbiculatum*, *Porotrichum* spp., *Hydrogonium taylori*, and *Gymnostomiella orcuttii*, as well as the endemic *Plagiochila galapagona* belong to this group.

The pampa near and above the inversion zone, as on Volcano Cerro Azul, southern Isabela, supports several species otherwise unknown on the islands. Most of them are temperate and of southern origin (see below). On Santa Cruz, where the inversion zone may possibly occur locally on the top of the barren exposed outcropping tors, *Polytrichum juniperinum* is the dominant moss.

As to individual species distributions, it seems that almost 75% of the liverworts are restricted to a single altitudinal zone whereas only 25% had a wider vertical distribution. The latter category includes, in part, the weedy, ubiquitous species which are seen on most major islands. The "ten most widespread liverwort species" (known from 6 or more different islands) are: *Bryopteris liebmanniana*, *Cheilolejeunea trifaria*, *Cololejeunea cardiocarpa*, *Frullania brasiliensis*, *F. ericoides*, *F. riojaneirensis*, *Lejeunea laete-virens*, *Plagiochila guilleminiana*, *Rectoleunea maxonii*, and the endemic Arid Zone-inhabiting *Riccia howellii*. All of these species produce copious spores and/or asexual propagula (gemmae, cladulae) and thus seem to spread easily (see Appendix). In contrast, about 30 species of liverworts are still known only from a single island. Three causes may be applicable:

1. *Our insufficient exploration of their potential habitats.* For instance, the Arid Zone species *Riccia iodocheila* and *Notothylas galapagensis* are only to be seen after short periods of heavy rain when the porous ash soils are moistened enough to stretch the small, thin thalli. These species are known from single collections and most likely are overlooked for this reason.

2. *Ecological restrictions.* Some species occur in habitats which are rare in Galapagos, such as (a) the borders of the few extant springs (see above), (b) the single permanent stream on the island of San Cristobal, along which the terrestrial liverworts *Alobiellopsis dominicensis*, *Cephalozioopsis intertexta*, *Neesioscyphus argillaceus* and *Symphyogyna brasiliensis* occur exclusively, (c) the vertical *Sphagnum-Cyathea* bogs (Itow 1974) on eroded moist crater edges (Santa Cruz, Cerro Azul on Isabela) where single species of the high Andean genera such as *Herbertus* and *Bazzania* are found (Weber et al. 1977), and (d) the dry, cool summit pampas above the inversion layer (IVb) found only on Isabela, where *Sauteria berteriana* and *Targionia stellaris* occur exclusively.

A special ecological group are the epiphyllous liverworts, mainly Lejeuneaceae, for which the natural Galapagos vegetation hardly provides suitable habitats except for the macrophyllous evergreen leaves of *Miconia robinsoniana*, which forms mossy scrub vegetation on Santa Cruz and San Cristobal. Since the colonization of the islands by man (about 150 years), cultivated trees and shrubs have been introduced and in some islands have largely eliminated the native vegetation of the moist zones.

Coffea arabica, *Psidium guajava*, *Citrus aurantiaca* and *Eugenia jambos* provide habitats for epiphyllic bryophytes and lichens. Where these species have been planted (Santa Cruz, San Cristobal, Floreana and southern Isabela's Sierra Negra) an epiphyllous vegetation has developed supporting about ten species of Lejeuneaceae. The poverty of the epiphyllous flora as compared to tropical mainland areas is no doubt due to the poor representation, until recent time, of potential habitats – macrophyllous tropical rain-forest and evergreen cultivars. The most successful leaf-colonizing species is *Leptolejeunea elliptica*, which is everywhere the dominant species in the orchards at 200–300 m (lacking, however, in the native *Miconia robinsoniana* scrub at higher elevations where *Drepanolejeunea* and *Colura* prevail). Epiphyllae known only from single localities are *Colura cylindrica*, *Drepanolejeunea bidens* and *Lejeunea trinitensis*.

3. *Dispersal capacity.* Loss of dispersability is a common phenomenon among island plants (Carlquist 1974) and animals. In unisexual bryophytes, plants of one sex may be absent, precluding the chances for dispersal by spores. Looking at the reproductive state of the liverworts on Galapagos, dispersability in general seems excellent: of the total flora about 85% produces spores and/or gemmae and about 40% of the species are bisexual. In comparison, the subantarctic Campbell Island, with an old, much richer liverwort flora (160 spp) supports only 10% bisexual species and consequently many species are considered relicts (Schuster 1979). While the excellent dispersal potential of the Galapagos liverworts argues for a young flora of recent arrival, it may also be significant that the majority of the species known thus far from a single Galapagos locality albeit not of restricted ecology, are unisexual and only known from sterile condition here (see Appendix). An example is *Cheilo-lejeunea rigidula*, a common neotropical species which here is only known sterile from the mossy *Zanthoxylum* woods of Pinta, where it is quite common! The apparent lack of an effective means of dispersal might have prevented this species from colonizing *Zanthoxylum* communities of other islands. Another example is *Syzygiella setulosa*, a common species of high montane regions of the continent (Bolivia). On Galapagos this species is only known from vertical, exposed summit rocks near the lake "El Junco" on San Cristobal, where it was collected in great quantity by Alban Stewart in the early 1900's and again by the authors in 1975.⁴ No further Galapagos localities are known although the species is abundant there (extensive reddish mats are visible from some distance away), and similar potential habitats are available on

⁴ The Stewart material was identified by Clark (1953) as *Syzygiella oppositifolia* (Spruce) Spruce, which is now being considered a synonym of *Jamesoniella rubricaulis* (Nees) Grolle (cf. Grolle, R., 1971, Feddes Rep. 82: 78). Our material was already distributed among herbaria as *Jamesoniella rubricaulis* when we realized that these plants do not belong to that species but to *Syzygiella setulosa* or some closely related taxon. Our plants seem to deviate somewhat from *S. setulosa* by the very large, knot-like, often confluent trigones of the leaf cells, the strongly papillose leaf cuticle and the very conspicuous stem cortex, consisting of 2–3 layers of strongly thickened, brownish cells contrasting with the much thinner walled, pale medullary cells. By lack of perianths the species is kept here under *S. cf. setulosa*. We are indebted to Dr. R. Grolle for his helpful suggestions concerning the identity of this interesting Galapagos liverwort.

nearby Santa Cruz, Isabela, San Salvador and Pinta. Perhaps the presence of the lake is the critical factor in the event that the species is distributed by waterfowl.

GEOGRAPHIC ELEMENTS: PHYTOGEOGRAPHY

On the basis of preliminary observations, we suggested earlier (Weber, 1966, Weber, et al. 1977) that the bryophyte flora of the Galapagos Islands is characterized by low endemism and high percentage of neotropical species, especially among the epiphytes. We are now able to give more precise figures, based on critical examination of over 95% of the collected species. Individual species ranges were taken from the most recent taxonomic revisions or, when lacking, from important floristic works (e.g. Fulford 1963-76; Schuster 1980). The following elements are distinguishable:

	MOSSES (102 spp.)	LIVERWORTS (102 species)
Endemics	6%	16%
Caribbean	20%	10% (West Indies and adjacent coasts of Central and South America)
Tropical Andean	0	6% (only known from Galapagos and adjacent mainland)
Neotropical	50%	48% (widespread in tropical America)
Wide tropical	9%	12% (known also from palaeotropics and sometimes entering warm-temperate regions)
Southern	1%	4% (outside Galapagos mainly in subtropical or temperate South America)
(Sub) Cosmopolitan	14%	4%

EDEMICS

While for seed plants, endemism amounts to about 50% of the indigenous Galapagos flora (Porter 1979: 436 indigenous taxa of which 223 are endemic), for spore plants this percentage is, not unexpectedly, much lower. Of 108 fern taxa only 8 are considered endemic. In comparison, relatively many endemic taxa are still recognized among Galapagos liverworts (16 = 16%) but very few among the mosses (6 = 6%). Although most of the endemics have been examined by specialists and have proven distinct from species described from the mainland or other areas, it is nevertheless quite feasible that some of them actually occur on the mainland but have yet to be collected there ("missing species"). A more intensive search for them in the bryophytically still very poorly known countries of Ecuador and Peru (Griffin & Gradstein 1982) is certainly called for.

Endemism is particularly high in *Riccia* (Jovet-Ast 1978) with three of the five species endemic, and *Plagiochila* (Inoue 1977, Inoue & Gradstein 1980) with five of the eight species endemic. In *Frullania*, the species-richest genus of Galapagos, there are two endemics among the fourteen common species and single endemic species occur in *Prionolejeunea* and *Taxilejeunea* (fide R. Grolle and M. Onraedt, species still undescribed), *Metzgeria* (Kuwahara 1979) and *Notothylas*. The endemic *Radula galapagona* Steph. and *Anthoceros simulans* Howe have not been studied critically recently and should be considered of doubtful status. Other so-called

endemic species, mainly species of Lejeuneaceae, *Frullania* and *Plagiochila*, have now been synonymized (see Appendix).

The distribution of endemic liverworts along the altitudinal gradient is shown in Fig. 3. It appears that, as percentages of the total flora, endemics are better represented in the open, drier regions than in the moist woodland zones where the highest species diversity occurs. Interestingly, the two endemic Lejeuneaceae are not in the mossy woodland zone where the family is most richly represented, but in the lower, drier evergreen woodlands and in the pampa, where the endemic *Prionolejeunea* is the only species of the family exclusively occurring there outside the forest.

Endemism in the mosses, in contrast to the Hepaticae, is extremely low, only 6%. The three endemic *Campylopus* species include two that are restricted to the wet zone (principally pampa) and one that occurs in the driest forested areas, where the only moisture is from fog. *C. galapagensis* is able to imbibe moisture extremely rapidly from humid air, a clear adaptation to the hostile environment. *Squamidium caroli* is a conspicuous and extremely abundant pendent moss, vying for dominance throughout the forested wet zones with *Zelometeorium patulum*. Crosby (correspondence) feels that this endemic may be synonymous with the extremely variable *S. nigricans*. *Hydrogonium taylori* is limited to a single spring on Floreana Island and has been collected twice, in 1934 and 1972. One would suppose that this relatively nondescript moss still awaits discovery somewhere in the Caribbean flora, and likely is not endemic. *Sphagnum stewartii* is extremely close to *S. perichaetiale* (= *S. erythrocalyx*), differing, according to Warnstorf, by lacking fibers in the stem epidermis. This matter needs to be studied by a competent sphagnologist. I consider the endemic status of the taxon questionable. All of the alleged endemics are, in one way or another, suspect.

It is tempting to correlate the relatively higher hepatic endemism in the drier areas with similar findings, for vascular plants. According to Porter (1979), 67% of the endemic vascular plants occur in the Arid zone. It is a striking fact (Weber et al. 1977, Weber & Lanier, 1977) that the lichen flora exhibits its endemism almost completely outside the moist woodland areas, with a very high proportion of endemics (species of coastal Chilean relationships) occurring on the exposed rocks of the coast or rarely near or above the inversion zone (Weber & Lanier, 1977). This phenomenon is indicative of a fundamentally different method utilized by crustose lichens to migrate to the islands. At the present time there is no evidence of them coming on pumice rafts; perhaps lichen propagula are picked up in feathers of oceanic birds in the preening process and disseminated by the same process or during moult. This is frankly conjectural.

Recent palaeobotanical findings by Colinvaux and Schofield (1976a, b) based on sediments in the El Junco lake of San Cristobal, indicate that in the past 25,000 years a dry period (tropical "ice age") of 15,000 years was followed by 10,000 years when a moister climate with more mesic habitats prevailed. Based on this evidence it might be presumed that the bryophyte-rich mossy forests of Galapagos were, during tropical Pleistocene dry periods, of much more restricted occurrence, if indeed they were at all developed, and so was the bryophyte vegetation. However, bryophytes may

survive rather extreme constrictions of their populations. The longer availability of the drier regions for natural selection and evolution may thus account for the much more elevated endemism in these areas, since aridity is a very positive stimulus for evolution (Stebbins 1952). As to bryophytes, one might at the same time look at the supposed endemics of the mossy woodlands with greater care in view of the only 10,000 years of their continuous, extensive presence in Galapagos and the supposed slow evolution of the group.

CARIBBEAN

This element comprises that group of Neotropical species found outside Galapagos only on Caribbean islands and adjacent coastal areas of North and Central America and northern South America. They might be considered coastal oceanic-Neotropical species. Their occurrence in Galapagos is usually at somewhat lower altitudes along the gradient, with optimal occurrence in the Transition Zone and the lower evergreen woodland zone (Fig. 3). Caribbean liverworts belong mainly to the family Lejeuneaceae, a reflection of the prominent occurrence of the family on the lower tropical islands and coasts: *Cololejeunea myriocarpa* (by some authors considered a subspecies of the wide-tropical *C. minutissima*), *Drepanolejeunea bidens*, *Lejeunea trinitensis*, *Neurolejeunea breutelii* and *Rectolejeunea maxonii*.

Tentatively placed in this group because they belong to genera in strong need of revision are *Aphanolejeunea gracilis* and *Brachiolejeunea bahamensis*. The only non-members of Lejeuneaceae in this element are *Alobiellopsis domingensis* from the permanent stream on San Cristobal, and *Radula fendleri*. Most of the species have excellent dispersal capacities by gemmae or caducous leaves (*Alobiellopsis*, *Rectolejeunea maxonii*, *Radula*), spores (*Brachiolejeunea bahamensis*) or both, except for *Neurolejeunea breutelii* and *Lejeunea trinitensis*, which are sterile on Galapagos. Significantly, the latter two are known only from single localities, whereas, copiously asexually-reproducing forms, e.g. *Rectolejeunea maxonii*, are among the most common Galapagos bryophytes.

The mosses shown an extremely strong Caribbean relationship. The Galapagos moss flora (see Appendix, Column 5) was compared with the published record for Colombia (Florschütz & Florschütz, 1979), Puerto Rico and the Virgin Islands (Crum & Steere, 1957), Ecuador (Steere, 1948), Florida (Breen, 1963), and Guatemala (Bartram, 1949). Even allowing for the imperfect record of the total Caribbean moss flora, it is very significant that 91% of the Galapagos mosses are found in the Caribbean area, and only 40% are known to occur in Ecuador. Virtually no species certain to have emanated from the Andes occur on the islands (in contrast with liverworts, see below).

We do not know when mosses first reached the Galapagos, but it is very likely that most of them came from Central America (a very high correlation exists between Galapagos and Guatemala) or from the Caribbean region. Even today, the arrival of Caribbean taxa may be via the northeastern trade winds prevailing during the

warm season. A small Caribbean element is also represented among the vascular plants (Svenson, 1946), and the Darwin finches have a close relative among the Caribbean avifauna (Lack, 1945). Very few of the Caribbean species found on the Galapagos Islands are represented on Cocos Island (e.g. *Fissidens garberi*, extremely abundant on huge stream boulders, and *Lepidopilum falcatulum*, abundantly epiphyllous there), which otherwise is located along the supposed migration route. However, this is probably explained by the extremely different highly tropical and extremely rain-drenched closed-forest and tall grass habitats not encountered anywhere on Galapagos (see below).

ANDEAN, NEO-TROPICAL AND WIDE-TROPICAL

These groups comprise essentially the "mainland taxa" that, with the prevailing eastern winds, have direct access via aerial transport to the islands and would therefore be expected to be the prevalent groups of bryophytes. Indeed, among liverworts they comprise about 70% of the total flora. Andean species are those known thus far only from tropical Andean countries – *Omphalanthus jackii* (Ecuador, Peru), *Colura cylindrica* (Ecuador only), *Radula episcia*, and three *Frullania* species from Ecuador and Peru: *F. laxiflora* and the pendulous *F. mathanii* and *F. aculeata* Tayl. (syn.: *F. acuminata* Steph.). The latter is a particularly common and striking species with long attenuate leaves resembling those of the moss *Campylium stellatum*. This species dominates in the epiphytic flora of the mossy *Miconia* scrub on Santa Cruz and San Cristobal.

Neotropical and wide-tropical species mainly comprise common widespread tropical taxa. Among wide-tropical species are included those that enter oceanic-temperate regions where they are sometimes characterized as Tertiary tropical relics: *Adelanthus decipiens*, *Lejeunea flava*, *Telaranea nematodes* and *Dumortiera hirsuta*.

The number of wide-tropical taxa is still small when compared with those known only from the neotropics but their number is expected to increase as more serious efforts are undertaken to compare paleotropical with neotropical species. A critical comparison between African and Asiatic taxa was undertaken by Pócs (1976) but a similar large-scale approach for neotropical taxa has not been carried out. For example, the common neotropical *Symphyogyna brasiliensis* Nees was recently shown by Grolle (1980) to be conspecific with the common African *S. lehmanniana* Mont. & Nees. It would not be surprising if, after a further comparison with entire-margined Asiatic taxa, the species would turn out to be of still wider tropical distribution. Similarly, *Leptolejeunea elliptica* (Lehm. & Lindenb.) Schiffn. has been considered a neotropical species. Schuster (1968) showed that it is similar to the Asiatic *L. acuta* Steph., at least on the species level. The species seems to be lacking in Africa, however (Van den Berghen, 1962). Consequently, *Leptolejeunea elliptica* sensu Schuster is the only "amphi-Pacific" liverwort of Galapagos. It should be noted that Bischler (1969), in her revision of neotropical *Leptolejeunea*, considered *L. elliptica* to be strictly neotropical and Asiatic material to be different at the species level!

In Fig. 3 a group of "tropical-montane" species are distinguished (32 liverworts) which, on the mainland, are mainly found above 1000 m in the mountain forests up to the paramos (see Gradstein & Hekking 1979 for altitudinal ranges in Colombia). Not surprisingly, these species occur in Galapagos only at the higher elevations and are mainly restricted to the mossy evergreen woodlands and the pampa. Some of them have only restricted occurrence on the islands: *Bazzania*, *Herbertus*, *Leptoscyphus*, *Odontoschisma*, *Syzygiella setulosa*, *Breutelia*, *Thuidium*, etc., whereas on the continent they are very common at high elevations (see below). The causes may be ecological or lack of effective dispersal means on Galapagos (except for *Odontoschisma* and *Leptoscyphus*, they are all sterile on Galapagos and without obvious means of vegetative reproduction).

SOUTHERN

The southern element comprises one moss – *Brachymenium fabronioides* (described from Argentina) and four species of Marchantiales which originate from southern subtropical or temperate regions and more or less disjunctly occur on Galapagos: *Marchantia berteroaana*, a weedy circumsubantarctic species (Schuster 1979) which recently has also been found in the high tropical Andes as far north as Colombia (Gradstein & Hekking 1979); *Sauteria berteroaana* and *Targionia stellaris*, known from the Chilean and Argentinian Andes (Menendez 1963). *Targionia stellaris* has recently been discovered in the high Andes of Peru (fide R. Grolle); and *Riccia plano-biconvexa*⁴ from dry, subtropical regions of Argentina, Paraguay and southern Brasil (Jovet-Ast 1978).

On Galapagos these species were found exclusively at high altitudes on the pampa (Fig. 3), two of them (*Sauteria*, *Targionia*) from the cool, dry pampa above the inversion layer on Isabela. Dispersability seems to be enhanced by copious production of spores (*Sauteria*, *Targionia*, *Riccia*) and gemmae (*Marchantia*). The occurrence of this element on Galapagos is not surprising; for vascular plants as well there is a relatively high percentage of temperate genera (*Pernettya*, *Aster*, *Salvia*) and as to animals there are the penguins and fur seals. As mentioned earlier there is a major element of southern South American coastal lichen genera and species as vicariads on the Galapagos. The presence of temperate-zone organisms, one of the characteristic features of Galapagos biogeography, is usually linked with the influence of the cold Humboldt Current and the relatively cool and dry resultant climate (van Balgooy 1971).

COSMOPOLITAN

Single collections have been made of the cosmopolitan *Marchantia polymorpha* and the subcosmopolitan *Anthoceros punctatus*, *Phaeoceros laevis* and *Fossombronia pusilla*. They were mainly found in mesic pampa on Isabela (Fig. 3). Several cosmo-

⁴ The species was recently discovered also in Costa Rica (Jovet-Ast 1981: Occ. Pap. Farlow Herb. 16: 113) and should therefore probably be revised to neotropical rather than southern.

politan mosses of a weedy nature are frequent: *Bryum argenteum*, *Ceratodon purpureus*, *Funaria*, *hygrometrica*, and *Weissia controversa*.

CHARACTERIZATION OF THE BRYOPHYTE FLORA OF THE GALAPAGOS ISLANDS

While for vascular plants a vast floristic literature is available allowing for whole-flora comparisons on a large scale for tropical regions (e.g. van Balgooy 1971), regional checklists for bryophytes are still severely lacking. It is only recently that professional bryologists have begun, in any numbers, to seriously collect these areas on long-term thorough surveys and the taxonomic problems of correlating disjunct floras are still very difficult (Verdoorn 1950). These factors limit the feasibility for a critical comparison of the Galapagos bryophytes with those of other islands or regions. Larsen & Holm-Nielsen's introductory statement at the Aarhus Symposium on Tropical Botany (1979) that tropical [vascular] floras are still poorly known, certainly holds much more for bryophytes than for vascular plants. Notwithstanding these limitations we will attempt to give a comparative characterization of the Galapagos Flora. At least the mosses appear to belong to predominantly well-known species less likely to be overlooked in the field than lejeuneoid hepatics, and the statistics gain reliability overall by this fact.

1. *Mainland South America.* Taking into account recent liverwort lists for Ecuador (Herzog 1952, Arnell 1962) and Colombia (Gradstein & Hekking 1979) it appears that about two-thirds of the Galapagos liverwort flora occurs on the adjacent mainland. If endemics and disjunct temperate species are not taken into account, this figure rises to over 80%, which shows that the bulk of the liverwort flora, as for vascular plants, was derived from the mainland to the east. A smaller portion supposedly came from the north (Caribbean coastal species) and very few, if any, came from the south (Southern Temperate species). Arrival would have taken place by the prevailing eastern trade winds. As discussed elsewhere in this paper, this is not true of the mosses, an indication that liverwort and moss propagula are not equally efficient.

Biogeographic connections with the western Pacific seem to be almost entirely lacking for all Galapagos plants as well as animals (Thornton [1971] mentions a single example of a Pacific land snail that happens to occur on Galapagos), except of course for the common pantropical species. Mention should be made of *Leptolejeunea elliptica* which, if delimited in a broad sense (Schuster 1968), is amphi-Pacific with a vicariant subspecies (ssp. *acuta* [Steph.] Schuster) in tropical East Asia and Australasia. This is the only possible case of amphi-Pacific distribution among bryophytes, and its uniqueness tends to suggest that the view of Bischler (above) may be more tenable.

When we compare the mainland flora with that of Galapagos, the mean number of species per genus, as expected, is lower on the islands than on the mainland. While for Galapagos liverworts (110 spp, 50 genera) the mean is 2.2 (Table 2), and for mosses 1.6, the rate is higher for Colombia although the available list of hepatics is only partly based on revised groups and the actual number of species (ca. 800) given by Gradstein & Hekking (1979) is probably twice the real number. A rate of about 3.5

TABLE 2. A comparison of liverwort generic/species richness on three tropical archipelagos.*

	Area, km ²	Max. Altitude, m	Max. annual rainfall, mm	Nr. of genera	Nr. of species	Genus to species ratio
Seychelles	250	900	4000	38	80	2.1
Samoa Is.		1850	5-6000	ca. 60	ca. 130	2.2
Galapagos Is.	7900	1700	3000	50	110	2.2

* Floristic data, also in Fig. 4, are based on this paper and on Arnell (1957), Bischler & Jovet-Ast (1979), Düll (1979, 1980), Evans (1930), Grolle (1978, 1980), Grolle & Schultze-Motel (1972), Herzog (1942) and Hill & Paton (1976).

(130 genera, 450 spp.) would probably be more realistic for Colombia. For mosses it is 3.8 based on Florschütz & Florschütz (1979).

Important mainland liverwort genera (rich in species) which are poorly represented on Galapagos, are:

	COLOMBIA	GALAPAGOS
<i>Bazzania</i>	35 spp.	1
<i>Calypogeia</i>	12	1
<i>Lophocolea</i>	14	1
<i>Leptoscyphus</i>	8	1
<i>Metzgeria</i>	27	2
<i>Symphyogyna</i>	8	1-2

Reasons for poor representation are probably lack of primary tropical forests on Galapagos (*Bazzania* is a particularly common element of these habitats on the mainland), lack of effective means of dispersal (*Bazzania*, *Calypogeia* and *Leptoscyphus*, for example, are usually unisexual and sterile, and vegetative propagula are not so common in these groups).

Compared with Colombia, which has the rich habitat diversity made possible by the Andes, the moss flora is depauperate and many families containing alpine specialists (e.g. Grimmiaceae, Andreaeaceae, Hypnaceae) are totally absent.

Mainland hepatic genera that are entirely lacking on Galapagos fall into two groups:

a. Genera that are characteristic of moist, cool mountain forests or paramos which are often rich in species on the mainland: *Anastrophyllum*, *Cephalozia*, *Lepidozia*, *Kurzia*, *Isotachis*, *Lepicolea*, *Trichocolea*, *Jamesoniella*, *Gongylanthus*, *Lethocolea*, *Lophozia*, *Jungermannia*, *Porella*, *Scapania*, *Jensenia*, *Riccardia*(!) and *Monoclea*. Lacking, of course, are exclusively tropic-alpine-temperate genera such as *Stephaniella*, *Marsupella* and *Gymnomitrium* (Gymnomitriaceae).

b. Genera characteristic of moist neotropical lowland forests. This group almost exclusively is made up of Lejeuneaceae: *Archilejeunea*, *Crossotolejeunea*, *Cyclolejeunea*, *Caudalejeunea*, *Mastigolejeunea*, *Hygrolejeunea*, *Odontolejeunea*, *Lopholejeunea*, *Stictolejeunea* and *Symbiezidium*. All of these occur in the rain forests of the Luquillo Mountains of eastern Puerto Rico (Fulford et al. 1971) while those spatiated are on

nearby Cocos Island (Clark 1953, Fosberg & Klawe 1966, Fournier 1966, unpublished collections of the second author) but lacking on Galapagos (previous Galapagos records of *Caudalejeunea*, *Mastigolejeunea*, *Lopholejeunea* and *Symbiezidium* are misidentifications). Both Puerto Rico and Cocos Island have diversified wet primary rainforests very different from the more mesic evergreen woodlands of Galapagos. Climatic factors probably account for the occurrence of these genera.

2. *Other tropical or temperate islands.* Comparing the Galapagos liverwort flora with that of the tropical Seychelles in the Indian Ocean, and Samoa, for which recent lists are available (cf. Table 2), it appears that the islands have only few species in common. While Galapagos shares four common, pantropical species with each (*Frullania ericoides*, *Cheilolejeunea trifaria*, *Lejeunea flava*, *Colura tenuicornis*), Samoa and Seychelles share many more (16) species notwithstanding their great geographical separation. While closer relationships among palaeotropical taxa may be one reason (see Pócs 1976), it should not be ruled out that the lack of critical taxonomic comparisons between neotropical and palaeotropical taxa also plays a role here.

While genus/species ratios for these islands are very similar (Table 2: 2.1-2.2), total number of known species differs although that for the Seychelles may be based on undercollecting and the smaller area, for the Galapagos on the drier climate. The large Mediterranean island of Crete, with an annual rainfall of maximally only 1200 mm has not more than 70 species of liverworts; the number would become lower

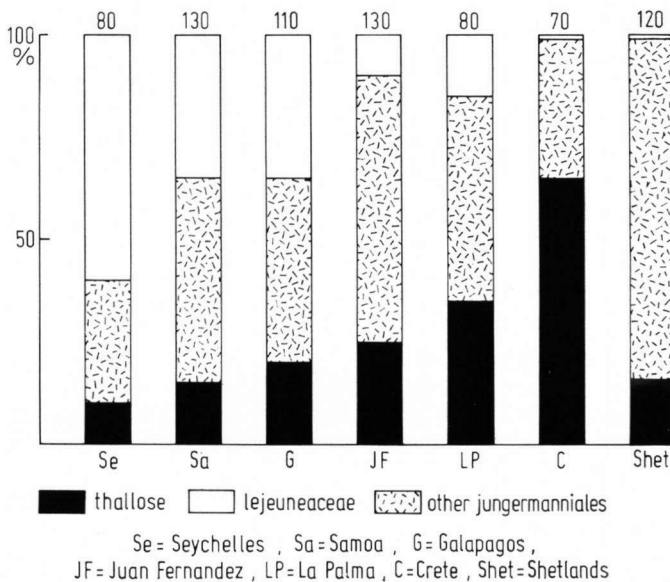


FIG. 4. A comparison of the Galapagos liverwort flora with that of other islands or island groups. Numbers at the top of each column indicate total number of liverwort species known for the individual islands or island groups. Floristic data are based on the same papers as cited under Table 2.

in even drier areas as is evident from Fig. 3.

When the percentage of thalloid and foliose liverworts (Fig. 4) for whole island floras are compared it appears that the percentage of Lejeuneaceae goes down drastically towards temperate regions whereas the percentage of thalloids rises, especially in the drier Mediterranean-Atlantic ones, e.g. La Palma, Canary Is., and Crete where Marchantiales dominate the liverwort flora (Jovet-Ast, Bischler & Beaudoin 1976). In temperate moist islands such as Juan Fernandez in the south and the Shetlands in the north (Fig. 4) thalloids are less abundant than in the Mediterranean with Metzgeriales, especially *Riccardia* spp. being common. *Riccardia* is entirely lacking on Galapagos and Marchantiales are the predominant thalloid types there (60% of all thalloid species). Much lower representation of Marchantiales is found on Samoa, which has otherwise a percentage of thalloid species similar to that of Galapagos. On the Seychelles Marchantiales are entirely lacking (Grolle 1978)! These data suggest a somewhat mesic subtropical character for the Galapagos liverwort flora notwithstanding the high representation of Lejeuneaceae.

LITERATURE CITED

- Arnell, S. 1957. Hepaticae collected during Dr. & Mrs. C. Skottsberg's second expedition to the Juan Fernandez Islands, Dec. 1954 – March 1955. *Ark. Bot.* 4: 1–21.
- . 1962. Contribution to the knowledge of the Hepaticae of Ecuador. *Svensk Bot. Tidskr.* 56: 334–350.
- Balgooy, M. M. J. van. 1971. Plant geography of the Pacific as based on a census of phanerogam genera. *Blumea suppl.* 4: 1–222.
- Bailey, K. 1976. Potassium-agron ages from the Galapagos Islands. *Science* 192: 465–466.
- Bartram, E. B. 1949. Mosses of Guatemala. *Fieldiana: Botany* 25: 1–442.
- Bischler, H. 1969. Le genre *Leptolejeunea* (Spruce) Steph. en Amerique. *Nova Hedwigia* 17: 265–350.
- , & S. Jovet-Ast. 1979. Nouvelles recoltes d'Hepatiques en Crete. *Rev. Bry. Lich.* 45: 45–60.
- Bowman, R. I. 1963. Evolutionary patterns in Darwin's finches. *Occ. Pap. Calif. Acad. Sci.* 44: 107–140.
- Breen, R. S. 1963. Mosses of Florida: 273 pp. illus. Univ. Florida press.
- Carlquist, S. 1974. Island biology: 660 pp. Columbia Univ. Press, New York.
- Clark, L. 1953. Some Hepaticae from the Galapagos, Cocos and other Pacific Coast islands. *Proc. Calif. Acad. Sci. ser. IV*, 27: 593–624.
- Colinvaux, P. A. & E. K. Schofield. 1976a. Historical ecology in the Galapagos Islands. I. A Holocene pollen record from El Junco Lake, Isla San Cristobal. *J. Ecol.* 69: 989–1012.
- & ———. 1976b. *Ibid.* II. A Holocene spore record from El Junco Lake, Isla San Cristobal. *J. Ecol.* 69: 1013–1026.
- Crum, H. 1957. A contribution to the moss flora of Ecuador. *Sv. Bot. Tidskr.* 51: 197–206.
- & W. C. Steere. 1957. The mosses of Puerto Rico and the Virgin Islands. *In Scientific Survey of Puerto Rico and the Virgin Islands Vol. 7*: 395–599. New York Academy of Sciences.
- Düll, R. 1979. Neue Uebersicht zur Moosflora der Insel Kreta (Aegaeis). *J. Bryol.* 10: 491–510.
- . 1980. Bryoflora und Bryogeographie der Insel La Palma, Canaren. *Cryptog., Bryol. Lichenol.* 1: 151–188.
- Evans, A. W. 1930. The thallose Hepaticae of the Juan Fernandez Islands. *In: The natural history of Juan Fernandez and Easter Islands (C. S. Skottsberg, ed.) Vol. II*: 551–586. Uppsala, Almqvist

& Wiksell,

- Florschütz-de Waard, J., & P. A. Florschütz. 1979. Estudios sobre criptogamas Colombianas III. Lista comentada de los Musgos de Colombia. *Bryologist* 82: 215-259.
- Fosberg, F. R., & W. L. Klawe. 1966. Preliminary list of plants from Cocos Island. *In* R. I. Bowman (ed.), *The Galapagos*: 107-189. Univ. California.
- Fournier, L. A. 1966. Botany of Cocos Island, Costa Rica. *In* R. I. Bowman (ed.), *The Galapagos*: 103-106. Univ. California.
- Fulford, M. 1963-1976. Manual of the leafy hepaticae of Latin America, parts I-IV. *Mem. N. Y. Bot. Gard.* 11: 1-535.
- , B. Crandall & R. Stotler. 1971. The ecology of an elfin forest in Puerto Rico, 15. A study of the leafy hepatic flora of the Luquillo Mountains. *J. Arn. Arb.* 52: 435-458.
- Gradstein, S. R. 1979. Vegetational zonation and bryophyte distribution on the Galapagos Islands. *Abstr. Bot. Budapest V*, 3: 47-50.
- , & W. H. A. Hekking. 1979. Studies on Colombian cryptogams, IV. A catalogue of the Hepaticae of Colombia. *J. Hattori Bot. Lab.* 45: 93-144.
- Griffin, D., & S. R. Gradstein. 1982. Bryological exploration of the tropical Andes: current status. *Beih. Hova Hedwigia* (in press).
- Grolle, R. 1978. Die Lebermoose der Seychellen. *Wiss. Zeitschr. Friedrich-Schiller Univ. Jena, Math-Nat. R.* 27: 7-17.
- . 1980a. Zur Kenntniss der Lebermoose von Samoa, 1. *Ibid.* 29: 637-648.
- . 1980b. Miscellanea hepaticologica 201-210. *J. Bryol.* 11: 325-334.
- Grolle, R., & W. Schultze-Motel. 1972. Vorläufiges Verzeichnis der Lebermoose von Samoa ["Somoa"]. *J. Hattori Bot. Lab.* 36: 75-89.
- Hamann, O. 1979. On climatic conditions, vegetation types and leaf size in the Galapagos Islands. *Biotropica* 11: 101-122.
- Herzog, T. 1942. Die foliosen Lebermoose der Juan Fernandez-Inseln und der Oster Insel. *In* C. S. Skottsberg (ed.), *The Natural History of Juan Fernandez and Easter Island*, Vol. II: 699-752. Uppsala, Almqvist & Wiksell.
- . 1952. Hepaticae euaodrenses a cl D: re Gunner Harling annis 1946-47 lectae. *Svensk. Bot. Tidskr.* 46: 62-108.
- Hill, M. O., & J. A. Paton, 1976. The bryophytes of Shetland: 59 pp. *Inst. Terrestr. Ecol. Great Britain.*
- Inoue, H. 1977. Notes on the Plagiochilaceae, VII. Four new species of the genus *Plagiochila* (Dum.) Dum. from the Galapagos Islands. *Bull. Nat. Sci. Mus. (Tokyo) B*, 3: 45-54.
- , & S. R. Gradstein. 1980. Notes on the Plagiochilaceae, IX. A review of the genus *Plagiochila* (Dum.) Dum. in the Galapagos Islands. *Ibid.* 6: 7-22.
- Itow, S. 1974. Fens and bogs in the Galapagos Islands. *Hikobia* 7: 39-52.
- Jovet-Ast, S. 1978. *Riccia* des Iles Galapagos. *Rev. Bry. Lich.* 44: 411-428.
- , H. Bischler & R. Beaudoin. 1978. Essai sur le peuplement hepatoologique de la region Meditteraneenne. *J. Hattori Bot. Lab.* 41: 87-94.
- Kuwahara, Y. 1979. *Metzgeria grandiflora* Evans, an endemic liverwort of the Galapagos Islands. *J. Jap. Bot.* 54: 265-271.
- Lack, D. 1945. The Galapagos Finches (Geospizinae). A study in variation. *Occ. Pap. Calif. Acad. Sci.* 21: vii + 1-151, pls. 1-4.
- Larsen, K., & L. B. Holm-Nielsen (ed.). 1979. *Tropical Botany*: 453 pp. Academic Press.
- Menendez, G. G. Hässel de. 1963. Estudio de las Anthocerotales y Marchantiales de la Argentina. *Opera Lilloana* 7: 1-297, figs. 1-105.
- Palmer, C. E., & R. L. Pyle. 1966. The climatological setting of the Galapagos. *In* R. I. Bowman (ed.), *The Galapagos*: 93-99. Univ. California.
- Pocs, T. 1976. Correlations between the tropical African and Asian bryofloras, I. *J. Hattori Bot. Lab.* 41: 95-106.

- Porter, D. M. 1979. Endemism and evolution in Galapagos Islands vascular plants. *In* D. Bramwell (ed.), *Plants and Islands*: 225-258. Academic Press.
- Schuster, R. M. 1968. Studies on Hepaticae, XXIV-XLIV. A miscellany of new taxa and new range extensions. *Nova Hedwigia* 15: 437-529.
- . 1979. On the persistence and dispersal of transantarctic Hepaticae. *Can. J. Bot.* 57: 2179-2225.
- . 1980. The Hepaticae and Anthocerotae of North America, Vol. IV: i-xviii, 1-1334, 774 figs. Columbia Univ. Press.
- Stebbins, G. L., Jr. 1952. Aridity as a stimulus to plant evolution. *Amer. Nat.* 86: 33-44.
- Steere, W. C. 1948. Contribution to the bryogeography of Ecuador. I. Review of the Musci previously reported. *Bryologist* 51: 65-167.
- Svenson, H. 1946. Vegetation of the coast of Ecuador and its relation to the Galapagos Islands. *Amer. J. Bot.* 33: 394-498.
- Thornton, I. 1971. *Darwin's Islands*: 322 pp. Nat. Hist. Press, New York.
- Van den Berghen, C. 1962. Lejeuneaceae epiphyllae d'Afrique (Note I). *Rev. Bry. Lich.* 32: 49-55.
- Verdoorn, F. 1950. The future of exotic cryptogamic botany. *Bryologist* 53: 1-7.
- Weber, W. A. 1966. Lichenology and bryology in the Galapagos Islands, with checklists of the lichens and bryophytes thus far reported. *In* R. I. Bowman (ed.), *The Galapagos*: 190-200. Univ. California.
- . 1976. Additions to the bryophyte flora of the Galapagos Islands. *Lindbergia* 4: 76-79.
- , S. R. Gradstein, J. Lanier & H. Sipman. 1977. Bryophytes and lichens of the Galapagos. *Noticias de Galapagos* 26: 7-11.
- , & J. Lanier. 1977. Lichens in the Galapagos Islands: 20 pp. (in Spanish). Charles Darwin Research Station.
- Werff, H. van der 1978. The vegetation of the Galapagos Islands: 102 pp. Thesis, Univ. Utrecht.
- . 1979. Conservation and vegetation of the Galapagos Islands. *In* D. Bramwell (ed.), *Plants and Islands*: 391-404. Academic Press.
- Wiggins, I., & D. M. Porter. 1971. *Flora of the Galapagos Islands*: 998 pp. Stanford Univ. Press.

APPENDIX: HEPATICAE, ANTHOCEROTAE AND MUSCI KNOWN FROM THE GALAPAGOS ISLANDS

Key to Abbreviations:

COLUMN 1: Locations (numerals refer of number of islands)

A = Alcedo crater (Isabela)	I = Isla Isabela
B = Bindloe	P = Isla Pinta
C = Cerro Azul (Isabela)	S = Isla Santa Cruz
D = Duncan	SC = Isla San Cristobal
F = Floreana	SS = Isla San Salvador (James)

COLUMN 2: Zones

I = Arid Zone, dry-season woodland	IIIb = Mossy open evergreen forest or scrub
II = Transition Zone, semi-deciduous woodland	IVa = Mesic pampa, below inversion line
IIIa = <i>Scalesia</i> Zone, closed evergreen woodland	IVb = Dry pampa, above inversion line

COLUMN 3: Substrates

c = corticolous	t = terrestrial
ph = epiphyllous	a = aquatic

s = saxicolous

COLUMN 4: Provenance

E = Endemic
 C = Cosmopolitan
 S = Southern
 TA = Tropical Andean
 TC = Caribbean

TN = Neotropical
 TP = Palaeotropical
 T = Wide Tropical
 m = mountainous

COLUMN 5: reproduction characteristics (Hepatics only)

g = with asexual reproduction (gemmae) in
 Galapagos

*sp = bisexual, with spores in Galapagos
 sp = unisexual, with spores in Galapagos

COLUMN 5: Floristic comparisons (Mosses only)

B: occurs in Florida (cf. Breen, 1963)

S: occurs in Ecuador (cf. Steere, 1948).

[B]: supplemental report for Florida

Ct: supplemental report for Ecuador (Crum,
 1957).

C: occurs in Puerto Rico (cf. Crum & Steere,
 1957)

Ba: occurs in Guatemala (Bartam, 1949).

F: occurs in Colombia (cf. Florschütz & Florschütz, 1979)

HEPATICAE

SPECIES (102)	1	2	3	4	5
LEJEUNEACEAE					
<i>Aphanolejeunea gracilis</i> Jov.-Ast	4	III	c, ph	TC	*sp, g
<i>Brachiolejeunea bahamensis</i> Evans	4	II, IIIa	c	TC	*sp
<i>B. densifolia</i> (Raddi) Evans	4	IIIb	c	TN	*sp
<i>Bryopteris liebmanniana</i> Lindenb. & Gott. (= <i>B. galapagona</i> Gott., <i>syn. nov.</i>)	7	III, IVa	c, s	TN	sp
<i>Ceratolejeunea cornuta</i> (Lindenb.) Schiffn.	2	IIIb	c	TN	sp
<i>Cheilejeunea rigidula</i> (Nees & Mont.) Schust.	P	III	c	TN	—
<i>C. trifaria</i> (Reinw., Bl. & Nees) Mizut.	7	III, IVa	c, s	T	*sp
<i>Cololejeunea cardiocarpa</i> (Mont.) Herz.	6	II, III, IVa	c, ph	T	*sp, g
<i>C. myriocarpa</i> (Nees & Mont.) Evans	3	II, IIIa	c, ph	TC	*sp, g
<i>Colura cylindrica</i> Herz.	S	IIIa	ph	TA	*sp, g
<i>C. tenuicornis</i> (Tayl.) Steph.	3	III, IVa	c, ph	T	*sp, g
<i>Dicranolejeunea axillaris</i> (Nees & Mont.) Schiffn. (= <i>Peltolejeunea galapagona</i> Steph., <i>syn. nov.</i>)	4	II, III, IVa	c, s	TNm	*sp
<i>Diplasiolejeunea rudolphiana</i> (Spruce) Schiffn.	3	II	c	T	*sp, g
<i>Drepanolejeunea bidens</i> Steph.	S	IIIa	ph	TC	sp, g
<i>D. inchoata</i> (Meisn.) Schiffn.	2	IIIa	c, ph	TN	g
<i>D. orthophylla</i> (Nees & Mont.) Bischl.	1	IIIb	c, ph	TN	g
<i>Lejeunea flava</i> (Sw.) Nees	5	III, IVa	c	T	*sp
<i>L. laetevirens</i> Nees & Mont.	8	II, III, IVa	c, s	TN	g
<i>L. setiloba</i> Spruce	C	II	c	TN	—
<i>L. trinitensis</i> Lindenb.	S	IIIa	ph	TC	—
<i>Lepidolejeunea punctata</i> (Herz.) Schust.	S	IIIb	c	TN	—
<i>Leptolejeunea elliptica</i> (L. & L.) Schiffn.	3	IIIa	ph	T	*sp, g
<i>Leucolejeunea xanthocarpa</i> (L. & L.) Evans	3	IIIb	c	Tm	*sp
<i>Marchesinia brachiata</i> (Sw.) Schiffn. (= <i>Lopholejeunea anderssonii</i> Steph., <i>Phragmicoma galapagona</i> Aongstr., <i>P. nigrescens</i> Aongstr. <i>syn. nov.</i>)	4	II, III, IVa	c, s	TN	sp

<i>Microlejeunea bullata</i> (Tayl.) Evans	4	III, IVa	c, ph	TN	g
<i>Neurolejeunea breutelii</i> (Gott.) Evans	S	IIIb	c,	TC	—
<i>Omphalanthus filiformis</i> (Sw.) Nees	5	IIIb	c, s	TNm	sp
<i>O. jackii</i> (Steph.) Gtadst.	2	III	c	TAm	*sp
<i>O. ovalis</i> (Lindenb. & Gott.) Gradst.	5	III	c	TNm	*sp
<i>Prionolejeunea sp. nov.</i> (fide R. Grolle)	C	IVa	c	E	—
<i>Rectolejeunea maxonii</i> Evans	6	III	c	TC	g
<i>Taxilejeunea asthenica</i> (Spruce) Steph.	S	IIIb	c	TN	*sp
<i>T. debilis</i> (L. & L.) Schiffn.	S	IIIb, IVa	c	TNm	sp
<i>T. dictyocalyx</i> (Spruce) Steph.	5	IIIb	c	TN	*sp
<i>T. pterogonia</i> (L. & L.) Schiffn.	3	IVb	c	TNm	*sp
<i>T. galapagensis</i> Onraedt	5	IIIa	c, ph	E	sp

Other JUNGERMANNIALES

<i>Adelanthus decipiens</i> (Hook.) Mitt.	4	IIIb, IVa	c, s	Tm	g
<i>Albiellopsis dominicensis</i> (Spruce) Fulf.	SC	III	t	TC	g
<i>Bazzania teretiuscula</i> (L. & G.) Trevis.	2	IIIb, IVa	c, s	TNm	—
<i>Calypogeia peruviana</i> Nees & Mont.	2	IIIb	t	TN	—
<i>Cephaloziaopsis intertexta</i> (Gott.) Schiffn.	SC	IIIb	t	TN	—
<i>Cylindrocolea rhizantha</i> (Mont.) Schust.	A	III	s	TN	—
<i>Frullania aculeata</i> Tayl. (= <i>F. acuminata</i> Steph., <i>syn. nov.</i>)	3	IIIb, IVa	c, s	TAm	sp
<i>F. arecae</i> (Spreng.) Gott.	S	IIIb	c	Tm	*sp
<i>F. atrata</i> (Sw.) Nees	3	IVa	c, s	TNm	sp
<i>F. brasiliensis</i> Raddi	6	II, III, IVa	c, s, ph	TN	sp
<i>F. darwinii</i> Gradst. <i>sp. nov.</i>	4	II, III	c	E	sp
<i>F. ericoides</i> (Nees) Mont.	8	I, II	c, s	T	sp
<i>F. gibbosa</i> Nees	2	II	c, s	T	—
<i>F. involuta</i> Hampe ex Steph.	2	IIIb	c, s	TCm	sp
<i>F. kunzei</i> (L. & L.) L. & L.	3	II, IIIa	c, s	TN	—
<i>F. laxiflora</i> Spruce	S	IIIb	c	TAm	*sp
<i>F. mathanii</i> Steph.	3	IIIb	c	TAm	sp
<i>F. mesophila</i> Gradst. <i>sp. nov.</i>	2	II	c	E	*sp
<i>F. obcordata</i> (L. & L.) L. & L. (= <i>F. galapagona</i> Aongstr., <i>syn. nov.</i>)	5	III	c	TN	*sp
<i>F. riojaneirensis</i> (Raddi) Spruce	6	II, III, IVa	c	TN	*sp
<i>Herbertus divergens</i> (Steph.) Herz.	3	IIIb, IVa	s	TNm	—
<i>H. pensilis</i> (Tayl.) Spruce	C	IVa	c	TNm	—
<i>Leptoscyphus porphyrius</i> (Nees) Grolle	S	IVa	c, s	TNm	g
<i>Lophocolea trapezoidea</i> Mont.	3	IIIb, IVa	c	TN	—
<i>Neesioscyphus argillaceus</i> (Nees) Grolle	SC	IIIb	t	TN	—
<i>Odontoschisma longiflorum</i> (Tayl.) Steph.	3	IIIb	c, s	TNm	g
<i>Plagiochila bursata</i> (Desv.) Lindenb.	4	IIIb, IVa	c, s	TNm	sp, g
<i>P. galapagona</i> Inoue	S	IIIb	t	E	—
<i>P. gradsteinii</i> Inoue	3	IIIb	c, s	E	g
<i>P. guillemianiana</i> Nees & Mont.	7	II, III, IVa	c, ph, s	TN	g
<i>P. inouei</i> Grolle	2	IVa	s	E	g
<i>P. scabrifolia</i> Inoue	C	IVa	s	E	—
<i>P. spinifera</i> Aongstr.	4	IIIb	c, s	E	sp
<i>P. subplana</i> Lindenb.	2	IIIb	c, s	TNm	—
<i>Radula boryana</i> (Web.) Nees	SC	IIIb	s, t	Tm	—

<i>R. episcia</i> Spruce	2	IVb	c, s	TAm	—
<i>R. fendleri</i> Gott.	S	IIIb	c	TC	g
<i>R. galapagona</i> Steph.	5	IIIb	c	TN	g
<i>R. mollis</i> Lindenb. & Gott.	4	IIIb	c	TNm	g
<i>R. ramulina</i> Tayl.	4	IIIb	c	TNm	g
<i>Syzygiella</i> cf. <i>setulosa</i>	SC	IVa	c, s	TNm	—
<i>Telaranea nematodes</i> (Gott. ex Aust.) Howe	4	IIIb	t	T	sp
<i>Tylimanthus fendleri</i> Steph.	2	IIIb	c	TNm	—
METZGERIALES					
<i>Fossombronia brasiliensis</i> Steph.	3	IVa	t	TNm	*sp
<i>F. pusilla</i> (L.) Dum.	A	IVa	t	C	*sp
<i>Metzgeria grandiflora</i> Evans	3	IIIb, IVa	c	E	sp
<i>M. myriopoda</i> Lindb.	2	IIIb	c	TN	g
<i>Symphyogyna brasiliensis</i> Nees	SC	IIIb	t	T	sp
MARCHANTIALES					
<i>Dumortiera hirsuta</i> (Sw.) R., Bl. & Nees	3	IVa	s	Tm	*sp
<i>Marchantia berteroa</i> L. & L.	S	IVa	t	S	sp, g
<i>M. chenopoda</i> L.	2	IVa	t	TN	sp, g
<i>M. polymorpha</i> L.	IA	IVa	t	C	sp, g
<i>Plagiochasma rupestris</i> (Forst.) Steph.	3	II, IVb	s	Tm	*sp
<i>Riccia howellii</i> Howe	6	I, IVa	t	E	*sp
<i>R. ianthina</i> Jov.-Ast	SS	I	s	E	*sp
<i>R. iodocheila</i> Howe	SS	IVa	t	TN	*sp
<i>R. limicola</i> Jov.-Ast	S	IVa	t	E	*sp
<i>R. plano-biconvexa</i> Steph.	I	IVa	t	S	*sp
<i>Sauteria berteroa</i> Mont.	C	IVb	t	S	*sp
<i>Targionia stellaris</i> Haessel	I	IVb	t	S	*sp
ANTHOCEROTAE					
<i>Anthoceros vegetans</i> Howe	3	IVa	t	TN	sp
<i>A. punctatus</i> L.	I	IVa	t	C	sp
<i>A. simulans</i> Howe	2	IV	t	E	*sp
<i>Dendroceros crispus</i> (Sw.) Nees	4	IIIb	c	TNm	—
<i>Notothylas galapagensis</i> Howe	2	I, II	t	E	*sp
<i>Phaeoceros</i> cf. <i>laevis</i> (L.) Prosk.	3	IV	t	C	sp

MUSCI

SPECIES (102)

BARTRAMIACEAE					
<i>Breutelia tomentosa</i> (Brid.) Jaeg.	I	IVa	t	TN	Ba, C, F, S
<i>P. sphaericarpa</i> (Hedw.) Brid.	4	III, IVa	t	TN	B, Ba, C, F, S
<i>P. uncinata</i> (Schwaegr.) Brid. (incl. <i>P. glaucescens</i> and <i>P. gracillima</i>)	5	III, IVa	t	TN	B, B, C, F
BRACHYTHECIACEAE					
<i>Brachythecium stereopoma</i> (Spruce ex Mitt.) Jaeg.	I	IVa	t	TN	Ba, C, F, S
<i>Rhynchostegium serrulatum</i> (Hew.) Jaeg. & Sauerb.	I, S	IIIa	s	TN	B

BRYACEAE

<i>Anomobryum filiforme</i> (Dicks.) Husnot	I	IIIb	s	C	Ba, F, S
<i>Brachymenium bulbiferum</i> Bartr.	I	IIIb	t	TC	C
<i>B. exile</i> (Dozy & Molk.) Bosch & Lac.	S, P	IIIb	t	TN	
<i>B. fabronioides</i> (C.M.) Par.	I	IIIb	t	S	
<i>B. macrocarpum</i> Card.	S, SS	II, IIIa	TC	s, t	B, Ba
<i>B. systylium</i> (C.M.) Jaeg. (<i>B. imbricatifolium</i> of reports)	5	II, IIIa	c	TN	B, C, F, S
<i>Bryum argenteum</i> Hedw.	5	II	s, t	C	Ba, B, C, F, S
<i>B. billardieri</i> Schwaegr.	F, S	IIIa	t	T	Ba, C, F
<i>B. coronatum</i> Schwaegr.	I	II	t	T	B, Ba, C, F, S
<i>B. cruegeri</i> Hampe in C.M.	3	IIIa	s	TN	B, Ba, C, F, S
<i>B. limbatum</i> C.M.	S	IIIa	s, t	TC	C
<i>Orthodontium pellucens</i> (Hook.) B.S.G.	P, SS	IIIa	t	TN	Ba, F, S
<i>Pohlia cruda</i> (Hedw.) Lindb.	I	IIIb	t	C	Ba
<i>P. elongata</i> Hedw.	S	IIIb, IVa	ct	C	
<i>P. nutans</i> (Hedw.) Lindb.	S	IIIa, IVa	st	C	
<i>Rhodobryum roseum</i> (Hedw.) Limpr.	I	IVa	t	TC	C, S

CALYMPERACEAE

<i>Calymperes donnellii</i> Austin	4	IIIb, IVa	c	TN	B, Ba, C, [S]
<i>C. erosum</i> C. M.	3	IIIb, IVa	t	TN	B, F
<i>C. richardii</i> C. M.	3	I, IIIb, IVa	st	TN	B, Ba, C, F
<i>Syrhropodon incompletus</i> Schwaegr.	6	III	cst	TN	B, Ba, C, F, S
<i>S. parasiticus</i> (Sw.) Besch.	4	III	c	TN	B, Ba, C, F, S
<i>S. prolifer</i> Schwaegr.	5	IIIb, IVa	cs	TN	B, Ba, C, F

CRYPHAEACEAE

<i>Schoenobryum</i> sp. (syn.: <i>Acrocryphaea</i>)	3	III	c		
---	---	-----	---	--	--

DICRANACEAE

<i>Campylopodium pusillum</i> (Schimp.) R. S. Williams	I	IVa	s	TN	Ba, C
<i>Campylopus anderssonii</i> (C. M.) Jaeg.	5	IVa	s	E	
<i>C. galapagensis</i> Frahm & Sipm.	6	I-IVb	cst	E	
<i>C. insularis</i> Bartr.	D, S	IIIb, IVa	t	E	
<i>C. pilifer</i> Brid.	S, SS	IIIb, IVa	s	T	C, F
<i>C. tallulensis</i> Sull. & Lesq.	3	IIIb, IVa	t	TN	
<i>C. zygodonticarpus</i> (C. M.) Par.	3	IIIb, IVa	t	TN	
<i>Dicranella</i> cf. <i>brachyblepharis</i> (C. M.) Mitt.	I, P	IVa	s	TC	Ba
<i>D. harrisii</i> (C. M.) Broth.	S	IVa	t	TC	C
<i>D. hilariana</i> (Mont.) Mitt.	S, SC	IVa	t	TN	B, Ba, C, F, S
<i>D. longirostris</i> (Schwaegr.) Mitt.	S	IIIa	t	TC	C
<i>D. perottetii</i> (Mont.) Mitt.	I	IVa	t	TC	C, F

DITRICHACEAE

<i>Ceratodon purpureus</i> (Hedw.) Brid.	I, S	IVa	t	C	Ba, F, S
<i>Ditrichum</i> spp. (several indet.)					

ERPODIACEAE

<i>Erpodium domingense</i> (Brid.) C. M.	P, S	II	S	TC	[B], Ba, C, F
--	------	----	---	----	---------------

FABRONIACEAE

<i>Fabronia polycarpa</i> Hook.	D	IVa	s	TC	Ba, C, F, S
---------------------------------	---	-----	---	----	-------------

<i>Helicodontium</i> sp. indet.	I	IVa	c		
FISSIDENTACEAE					
<i>Fissidens asplenoides</i> Hedw.	3	IIIa	s	TC	C, F, S
<i>F. garberi</i> Lesq. & James	3	IIIa	ct	TN	B, C
<i>F. guianensis</i> Mont.	3	IIIa	s	TN	
<i>F. intermedius</i> C. M.	I	IVa	t	TN	
<i>F. kegelianus</i> C. M.	SC	II	t	TN	B, C
<i>F. repandus</i> Wils.	5	IIIa	t	TN	B, Ba, C, F, S
<i>F. reticulosus</i> (C. M.) Mitt.	I, S	IIIa	t	TN	Ba
<i>F. stenopteryx</i> Besch.	I	IVa	s	TN	C
<i>F. weirii</i> Mitt.	3	IIIa	st	TN	Ba, C
FUNARIACEAE					
<i>Entosthodon bonplandii</i> (Brid.) Mitt.	I	IVa	t	TN	Ba, C, F
<i>Funaria hygrometrica</i> Hedw.	S, SC	IVa	t	C	B, Ba, C, F, S
HOOKERIACEAE					
<i>Cyclodictyon albicans</i> (Hedw.) Broth.	3	IIIa	ct	TN	Ba, C, F, S
<i>Daltonia lindigiana</i> Hampe	S	IIIb	c	TN	F, S
<i>D. longifolia</i> Tayl.	3	IIIb	c	TN	Ba, C, F, S
<i>Hookeriopsis</i> sp.	S, SC	IIIb	s		
<i>Crossomitrium orbiculatum</i> C. M.	S	IIIa	t	TC	C
<i>Lepidopilum falcatum</i> C. M. (= <i>Crossomitrium patrisiae</i>)	I	IIIb	t	TC	Ba, F, S
<i>L. aff. biductulum</i>	S	IIIb	c		
LEUCOBRYACEAE					
<i>Leucobryum albidum</i> (P.-B.) Lindb.	S	IIIb	t	T	B, Ba, C
<i>Octoblepharum albidum</i> Hedw.	5	III	c	T	B, Ba, C, F, S
LEUCODONTACEAE					
<i>Leucodontopsis geniculata</i> (Mitt.) Crum & Steere	I, S	III III	t	TN	B, Ba, C, F
METEORACEAE					
<i>Papillaria nigrescens</i> (Hedw.) Jaeg.	5	III	c	T	B, Ba, C, F, S
<i>Squamidium carolii</i> (C. M.) Broth.	6	IIIB	c	E	
<i>S. leucotrichum</i> (Tayl.) Broth.	5	III	c	TN	Ba, C, F, S
<i>Zelometeorium patulum</i> (Hedw.) Manuel	5	II, IIIa	c	T	B, Ba, C, F, S
NECKERACEAE					
<i>Porotrichum insularum</i> Mitt.	S	II, IIIa	s	TC	C
<i>P. plicatum</i> Mitt.	S, SC	III	c, t	TN	Ba, C, F
ORTHOTRICHACEAE					
<i>Grouttella mucronifolia</i> (Hook. & Grev.) Crum & Steere	6	IIIa	c	TN	B, Ba, C, F
<i>G. tomentosa</i> (Hornsch.) Wijk & Marg.		IIIa	c, s	TN	Ba, F
<i>Macromitrium cirrosom</i> (Hedw.) Brid.	4	IVa	c	TN	Ba, C, F
<i>M. guatemalense</i> C. M.	I, S	III	c	TN	Ba
<i>M. homalacron</i> C. M.	S	IIIb	c	TC	Ba
<i>M. longifolium</i> (Hook.) Brid.	5	IIIb	c	TN	Ba, F, C
PLAGIOTHECIACEAE					
<i>Isopterygium cf. secundum</i> R. & C.	S	IVb	t		

<i>I. tenerum</i> (Sw.) Mitt.	I, S	IVa	t, a	TN	C, F, S
<i>Mittenothamnium diminutivum</i> (Hampe) E. G. Britt.	I, S	IIb, IVa	s, t	TN	B, Ba, C, F
<i>Stereophyllum papilliferum</i> Mitt.	3	II, IIIa	s, c	TN	S
<i>S. radiculosum</i> (Hook.) Mitt.	SC	II	c	TN	B, C
POLYTRICHACEAE					
<i>Polytrichum juniperinum</i> Willd. ex Hedw.	S	IVa	t	C	Ba, F, S
POTTIACEAE					
<i>Anoetangium aestivum</i> (Hedw.) Mitt. (incl. <i>A. euchloron</i>)	4	II, IIIb IVa	s, t	C	Ba, S
<i>Didymodon australasiae</i> (Hook. & Grev.) Zander	I	IVb	t	C	Ba, F, S
<i>D. tophaceus</i> (Brid.) Garov.	I	IIIb	t	C	Ba
<i>Gymnostomiella orcuttii</i> Bartr.	3	II	s, t	TC	B, C
<i>Hydrogonium taylori</i> W. A. Weber	F	II	t, a	E	
<i>Hymenostomum breutelii</i> (C. M.) Broth.	3	II	t	TN	C
<i>Hyophila microcarpa</i> (Schimp. ex Besch.) Broth.	6	I, II	t	TN	Ba, C
<i>H. involuta</i> (Hook.) Jaeg.	5	II, IIIa	s	T	B, Ba, C, F, S
<i>Pseudocrossidium replicatum</i> (Tayl.) Zander (= <i>Barbula replicata</i>)	F, I	II, IVb	s, t	TN	Ba, F, S
<i>Rhamphidium dicranoides</i> (C. M.) Bartr.	SC	IIIa	t	TN	Ba, C, S
<i>Scopelophila ligulata</i> (Spruce) Spruce	P, S	IVa	s	T	Ba, S
<i>Tortella humilis</i> (Hedw.) Jenn.	6	II, IIIb	s, t	C	B, C
<i>Trichostomum jamaicense</i> (Mitt.) Jaeg.	5	II, IIIa, IVa	t	TC	Ba, B, C
<i>Trichostomum perviride</i> Broth.	I, P	II	t	TC	
<i>Weissia controversa</i> Hedw.	F, I	I, II	t, s	C	Ba, B, C, F, S
PRIONODONTACEAE					
<i>Prionodon densus</i> (Hedw.) C. M.	S	IIIa	c	TN	Ba, F, S
RACOPILACEAE					
<i>Racopilum tomentosum</i> (Hedw.) Brid.	4	III	t	T	B, Ba, C, F, S
SEMATOPHYLLACEAE					
<i>Sematophyllum adnatum</i> (Michx.) E. G. Britt.	5	III	c, t	TN	B
<i>S. caespitosum</i> (Hedw.) Mitt.	5	III	c, t	T	B, Ba, C, F, S
SPHAGNACEAE					
<i>Sphagnum aleggense</i> Warnst.	S	IVa	t, a	TN	
<i>S. cuspidatum</i> Ehrh.	S	IVa	t, a	C	B, C, F
<i>S. perichaetiale</i> Hampe	I, S	IVa	t, a	TN	B, C, F
<i>S. stewartii</i> Warnst.	S	IVa	t, a	E	
<i>S. (Inophloea) sp.</i> indet.	S	IVa	t, a		
THUIDIACEAE					
<i>Thuidium recognitum</i> (Hedw.) Lindb. <i>var. delicatulum</i> (Hedw.) Warnst.	I	IVa	t	T	B, Ba, F, S

Addendum: *Cephaloziella* of the Galapagos Islands, identified by J. Vána, Prague.

<i>Cephaloziella</i> cf. <i>antillana</i> (Spruce) Fulf. (sterile)	SC	IIIb	c	TC	—
<i>C. granatesis</i> (Jack) Fulf.	2	IVa	s	TNm	*sp
<i>C. cf. divaricata</i> (Sm.) Schiffn. (sterile)	4	IVa	t	C?	—