

MAGYAR AFRIKA TÁRSASÁG
AFRICAN-HUNGARIAN UNION



AHU MAGYAR AFRIKA-TUDÁS TÁR
AHU HUNGARIAN AFRICA-KNOWLEDGE DATABASE

PÓCS, Tamás

The Distribution and Origin of the Foliicolous Bryophyta in the Indian Ocean Islands

Eredeti közlés /Original publication:

Abstracta Botanica, 1997, Vol. 21., No. 1., 123–134, pp.

Elektronikus újraközlés/Electronic republication:

AHU MAGYAR AFRIKA-TUDÁS TÁR – 000.003.241

Dátum/Date: 2018. november / November.

filename: pocs_1997_IndianOceanIslands

Ezt az információt közlésre előkészítette

/This information prepared for publication by:

B. WALLNER, Erika és/and BIERNACZKY, Szilárd

Hivatkozás erre a dokumentumra/Cite this document:

PÓCS, Tamás: The Distribution and Origin of the Foliicolous Bryophyta in the Indian Ocean Islands, *AHU MATT*, 2018, **pp. 1–14. old.**, No.

000.003.241, <http://afrikatudastar.hu>

Eredeti forrás megtalálható/The original source is available:

Közkönyvtárakban / In public libraries

Kulcsszavak/Key words

African studies in Hungary,

Abstract: see above

AZ ELSŐ MAGYAR, SZABAD FELHASZNÁLÁSÚ, ELEKTRONIKUS,
ÁGAZATI SZAKMAI KÖNYV-, TANULMÁNY-, CIKK-
DOKUMENTUM- és ADAT-TÁR/THE FIRST HUNGARIAN FREE
ELECTRONIC SECTORAL PROFESSIONAL DATABASE FOR BOOKS,
STUDIES, COMMUNICATIONS, DOCUMENTS AND INFORMATIONS

* magyar és idegen – angol, francia, német, orosz, spanyol, olasz és szükség szerint más – nyelveken készült publikációk elektronikus könyvtára/
writings in Hungarian and foreign – English, French, German, Russian, Spanish, Italian and other – languages

* az adattárban elhelyezett tartalmak szabad megközelítésűek, de olvasásuk vagy letöltésük regisztrációhoz kötött/the materials in the database are free but access or downloading are subject to registration

* Az Afrikai Magyar Egyesület non-profit civil szervezet, amely az oktatók, kutatók, diákok és érdeklődők számára hozta létre ezt az elektronikus adattári szolgáltatását, amelynek célja kettős, mindenekelőtt sokoldalú és gazdag anyagú ismeretekkel elősegíteni a magyar afrikánisztikai kutatásokat, illetve ismeret-igényt, másrészt feltárni az afrikai témájú hazai publikációs tevékenységet teljes dimenziójában a kezdetektől máig./The African-Hungarian Union is a non-profit organisation that has created this electronic database for lecturers, researchers, students and for those interested. The purpose of this database is twofold; on the one hand, we want to enrich the research of Hungarian Africa studies with versatile and plentiful information, on the other hand, we are planning to discover Hungarian publications with African themes in its entirety from the beginning until the present day.

Key words: Endemism, Epiphylls, Dispersal, Indian Ocean, Insularity, Madagascar, Mascarenes, Seychelles

Abstract: The epiphyllous bryoflora of Madagascar and neighbouring islands contains the highest number of species among the African floristic regions (91 typically epiphyllous and 62 facultatively epiphyllous species), with a rate of 32.6% endemism (Madagascar itself with 37.4% endemism), which is high compared to other island floras (Cuba has 11.4% and Galapagos Islands have 16% endemism among liverworts and even less among epiphylls).

The affinity between the epiphyllous floras of the island-groups was calculated and the geographical elements of their bryofloras compared to each other and to that of the Usambara Mountains in continental Africa. The continental African and Asian influence and the rate of endemism and the insularity indices vary from island to island. Interestingly, the floristic affinity in many cases is greater between the small islands far from each other than between them and Madagascar.

The obtained data suggest that the epiphyllous bryoflora of the archipelago could evolve mostly during a period when the terrestrial link had already ceased between the dissected parts of Gondwanaland, but they (especially India, the ancient Seychelles subcontinent and Madagascar) were much closer to each other than they are nowadays. These conditions prevailed during the Cretaceous. Most of the endemic species of the area possibly evolved since that time more from the dispersed elements than from the pre-Cretaceous archaic Gondwanan stock.

The distribution and origin of the foliicolous bryophyta in the Indian Ocean Islands

Tamás Pócs

Eszterházy Teachers' College, Dept. of Botany, EGER, Pf.43, H-3301, HUNGARY

Key words: Endemism, Epiphylls, Dispersal, Indian Ocean, Insularity, Madagascar, Mascarenes, Seychelles

Abstract: The epiphyllous bryoflora of Madagascar and neighbouring islands contains the highest number of species among the African floristic regions (91 typically epiphyllous and 62 facultatively epiphyllous species), with a rate of 32.6% endemism (Madagascar itself with 37.4% endemism), which is high compared to other island floras (Cuba has 11.4% and Galapagos Islands have 16% endemism among liverworts and even less among epiphylls).

The affinity between the epiphyllous floras of the island-groups was calculated and the geographical elements of their bryofloras compared to each other and to that of the Usambara Mountains in continental Africa. The continental African and Asian influence and the rate of endemism and the insularity indices vary from island to island. Interestingly, the floristic affinity in many cases is greater between the small islands far from each other than between them and Madagascar.

The obtained data suggest that the epiphyllous bryoflora of the archipelago could evolve mostly during a period when the terrestrial link had already ceased between the dissected parts of Gondwanaland, but they (especially India, the ancient Seychelles subcontinent and Madagascar) were much closer to each other than they are nowadays. These conditions prevailed during the Cretaceous. Most of the endemic species of the area possibly evolved since that time more from the dispersed elements than from the pre-Cretaceous archaic Gondwanan stock.

Introduction

The Indian Ocean Archipelago near East Africa (Figure 1) offers a unique opportunity to analyse the composition of its biota. Their parts are very different in age, geology and in climatic conditions. Therefore the islands form a unique open air laboratory of evolution. If we analyse the geographic composition of an ecologically uniform and taxonomically relatively well known group, as the foliicolous bryophyta are, we can hope to reveal interesting data on their evolutionary history, dispersal and distribution.

The western Indian Ocean islands near East Africa can be classified geologically into four groups (Renvoize 1979).

- Old parts (Precambrian age) of the former Gondwanaland: Madagascar and the Seychelles
- Young volcanic origin (from 8 million years ago to present): The Comoros, Réunion, Mauritius and Rodriguez

- Elevated coral islands (from the late interglacial, deposited on volcanic basement): Aldabra island group
- Sea level reefs or sand cays (quite recent surface): Europe Island, Farquihar, the Amirantes, Coetivy, Agalega, Tromelin, Cargados, Carajos and others.

From our point of view only the two first groups are to be taken in account, as on the coral islands and sand cays there is no forest vegetation on which epiphylls can occur (Vesey-Fitzgerald 1942). By its large size (fourth largest island of the world its 587,041 km² area) and very varied geology and climate, Madagascar offers by far the most diverse habitat and has the richest flora. Apart from the dominating Precambrian gneisses and intrusive granites, during the Cretaceous and even in the Pleistocene, intensive volcanic activity covered large areas with basaltic lava, approaching an altitude of 3,000 m. In addition, since the Carboniferous (and especially during the Jurassic) large limestone or other sedimentary deposits covered especially the

western half of the island (Balázs 1983). From these deposits the harder granite inselbergs with steep slopes protrude at many places. The climate is dry in the southwest and very wet in the northeast, so the vegetation varies from dry thornbush to the wettest rainforests.

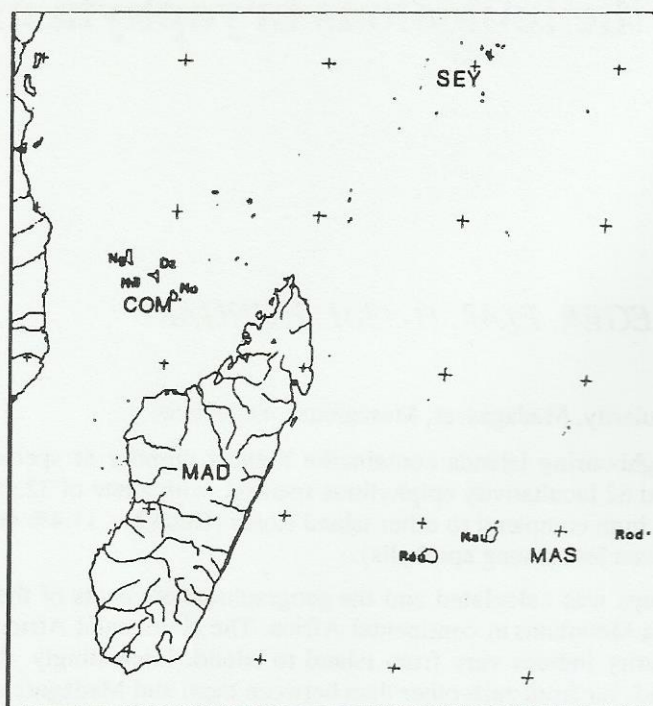


Figure 1: Map of the western Indian Ocean islands.

COM = Comoro Islands, Dz = Dzuan (Anjouan, Johanna), MAD = Madagascar, MAS = Mascarene islands, MAU = Mauritius, Mo = Maore (Mayotte), Mw = Mwali (Mohéli), Ng - Ngazidja (Grand Comoro), Réu = Réunion, Rod = Rodriguez, SEY = Seychelles Islands

The Comoro Islands form an archipelago of 2136 km² land area between Africa and the NW coast of Madagascar, but have never been in contact with them. They consist of four large and many small islets, which subsequently developed above a hot spot. Ngazidja (Grande Comore) is the largest and highest (Karthala 2,263 m), and the youngest, with active recent vulcanism. The southwestern slopes of Karthala enjoy high rainfall (above 5,000 mm) with luxuriant rainforests, while the eastern and northern ends are bordered by a dry deciduous forest belt with baobab (*Adansonia digitata*). Mwali (Mohéli) Island is the smallest, but much older (3-4 million years), with a mountain range of 790 m, covered by rainforest. Ndzuani (Anjouan or Johanna Island) has similar age (3 million years) and medium altitude (1,595 m) with rich rainforest cover except the dry eastern belt. Maore (Mayotte) is the oldest (5-8 million years) and the most eroded (only 660 m

high) consisting of sunken volcanoes of which only the calderas emerge, surrounded by a huge coral atoll. The greatest part of the island has semi-arid climate with dry deciduous forest. Wet forests cover very little area, mostly on the summit ridges.

The Seychelles are small outstanding remnants of a former large subcontinent stretching now under the sea level from the present granite island group almost to Mauritius (the "Seychelles Bank"). At present they only have 404 km² land surface. Their alkaline granite partly consists of Mahé, Praslin, Silhouette, La Digue, Curieuse and some 20 other smaller islands. Even the largest (Mahé), which reaches almost 1,000 m in altitude, is only 30 km long and 4-7 km wide. Precipitation is rather high (2-4,000 mm) in the islands and rainforests dominated the original vegetation, which is now very much intermixed with naturalized species. Praslin island has stands of the very isolated, ancient monotypic and endemic palm *Lodoicea maldivica*, which forms a lowland rainforest-like association with other endemic Palmae and Pandanus species.

The Mascarenes consist of two larger island and one smaller islet. Réunion is a relatively young (1-3 million years), round island of 2,500 km² area, built up of an ancient volcano system (Piton des Neiges, 3070 m) with three huge calderas and a recent and very active volcano (Piton de la Fournaise, 2632 m). The surface is rugged, dissected by enormous gorges with 1-2,000 m high walls and with huge waterfalls. Precipitation is very high (up to 10,000 mm in places) except for a narrow western strip which receives less than 750 mm. Luxuriant montane rainforests are still extant over large areas, but the lowland forests are mostly replaced by sugarcane plantations. Mauritius is older (4-8 million years), with a very eroded surface (2,046 km²). Only steep inselbergs now pop up from the sea of sugar-cane fields and there are little remnant fragments of the original forest cover, except for the south, where in the Macchabe Nature Reserve a larger montane forest area survived. Similar to Réunion, the island is about 60 km in diameter. Rodriguez island is much smaller and younger (1.5 million years), mostly with secondary vegetation.

Common properties of the above islands are the oceanic climate with lowered vegetation belts (mossy cloud forests often from 600 m altitude upwards), high rate of endemism both on granitic and on volcanic islands, and strong human impact

including serious deforestation. Especially on the smaller islands several introduced woody plants are very competitive against the indigenous species, invading the rainforests and replacing the less competitive native forest trees and shrubs. The phenomenon is typical for smaller islands with low native species diversity and unsaturated niches. Among the cryptogams this phenomenon (invasion of secondary species) was not observed, but the relative low species number with large niche width is obvious.

Material and methods

To analyse the epiphyllous (foliicolous) bryoflora the author used his own observations based on epiphyllous relevés and the available literature records. The geographical distribution type was established for each foliicolous species, based on its extant range of distribution (Table 1). The distribution types were then analysed in each larger island or island group (Table 2, figs 2-3) and compared to the epiphyllous bryoflora of Usambara Mountains in mainland Africa.

The rate of species endemism was counted for each island or island group (Table 3). As the level of revision in the different genera is very different, "proven" endemics (in the sense of Pócs 1988, Gradstein et al. 1994) at this moment can not be distinguished from the "potential" ones. Using the above data and the species/genus ratio (Table 4), Tryon's (1979) insularity index was given for each island (Table 5). Finally the affinity between foliicolous floras of the islands and the Usambara I mountains was counted using Jaccard's coefficient (Table V).

Results and conclusions

The distribution of epiphyllous species (see tables 1-2 and figure 2)

The presently known epiphyllous bryophyte flora is enumerated in Table I. The list is not exhaustive - many of our and some other epiphyllous collections are not yet identified. More details about the distribution of species can be found, among others, in the publications of Herzog (1947), Arnell (1965), Jovet-Ast (1956, 1958, 1959, 1983), Onraedt (1977), Tixier (1976, 1977, 1979a, 1979b, 1984, 1985), Grolle (1974, 1975, 1978), Grolle & Onraedt (1974), Pócs (1984, 1993, 1995) and in the numerous papers on African epiphyllous liverworts (often dealing with taxa from the islands), by E.W. Jones and by C. Vanden Berghen. A full list of all previously published records for the area, with taxonomic annotations and complete bibliography is supplied by Grolle (1995).

The epiphyllous flora of the Indian Ocean islands, consisting of 91 true epiphyllous liverwort species, is relatively rich compared to areas similar or even larger in size, and the richest compared to other African floristic regions (West Africa has 62, Oceania 105, lowland South America 106, the Andes 115, Meso-America with Mexico 125, Melanesia with New Guinea 167 species - calculation made by Pócs 1996, using all available literature sources). Its relative richness can be explained with the old age and early isolation of the archipelago and its islands. Some of them, like Madagascar, broke away from the former Gondwanaland very early, about 140 million years ago. Some other islands, like the Comoros, were never connected to any other land mass, while the Seychelles are remnants of a former, much larger subcontinent.

Table 1: The distribution of the Indian Ocean's epiphylls compared to the foliicolous bryoflora of the Usambara Mts. in continental East Africa (Species marked by "*" are true epiphylls)

HEPATICAE

	SEY	COM	MAD	REU	MAU	USB	Distribution
* <i>Aphanolejeunea exigua</i>	.	+	+	.	.	+	Afr.-Amer.
* <i>A. microscopica</i>	.	.	+	.	.	.	Trop. Afr.
* <i>A. moramangae</i>	.	+	+	.	.	+	EAfr.-LEM.
<i>Capillolejeunea mascarena</i>	.	+	+	.	+	.	Subend.
<i>Caudalejeunea hanningtonii</i>	.	.	+	.	.	.	Trop. Afr.
<i>C. lewallei</i>	.	.	+	.	.	+	Trop. Afr.
<i>C. recurvistipula</i>	.	+	+	.	.	.	Trop. Asla
<i>Ceratolejeunea belangeriana</i>	.	+	+	+	+	.	Trop. Asla
<i>C. jungneri</i>	+	.	+	.	.	+	Trop. Afr.

<i>C. papuliflora</i>	.	+	.	.	.	MAD. end.
<i>C. variabilis</i>	.	.	+	+	+	Subend.
<i>Cheilolejeunea decursiva</i>	.	+	+	+	+	Palaeotr.
<i>C. krakakammae</i>	.	+	+	+	+	EAfr.-LEM.
<i>C. montagnei</i>	.	+	+	+	+	Trop. Afr.
<i>C. pluriplicata</i>	.	.	+	.	.	EAfr.-MAD
* <i>C. serpentina</i>	+	+	+	+	+	Palaeotr.
* <i>C. surrepens</i>	+	+	+	+	+	Trop. Afr.
* <i>Cladolejeunea aberrans</i>	USB. end.
* <i>Cololejeunea adnata</i>	.	.	+	.	.	MAD. end.
* <i>C. africana</i>	Trop. Afr.
* <i>C. andapania</i>	.	.	+	.	.	MAD. end.
* <i>C. ankaiana</i>	.	.	+	.	.	MAD. end.
* <i>C. amaniensis</i>	USB. end.
* <i>C. appressa</i>	+	+	+	+	.	Pantrop.
* <i>C. auriculata</i>	+	.	+	.	.	W Afr.-LEM.
* <i>C. bandamiae</i>	.	+	.	.	.	COM. end.
* <i>C. bebourensis</i>	.	+	.	+	.	Subend.
* <i>C. bidentula</i>	.	.	+	+	+	Subend.
* <i>C. borbonica</i>	.	.	.	+	.	MAD. end.
* <i>C. bosseriana</i>	.	.	.	+	.	EWU. end.
* <i>C. camusii</i>	.	.	+	.	.	MAD. end.
* <i>C. capuronii</i>	.	.	+	.	.	MAD. end.
<i>C. cardiocarpa</i>	.	.	+	.	.	Pantrop.
* <i>C. ceatocarpa</i>	.	.	.	+	.	Trop. AsO.
* <i>C. cristata</i>	.	.	+	.	+	Trop. Afr.
* <i>C. cuneata</i>	.	+	+	+	.	Palaeotr.
* <i>C. decemplicata</i>	.	.	+	+	.	Subend.
* <i>C. derooinii</i>	.	.	+	.	.	MAD. end.
* <i>C. diplasolejeuneoides</i>	.	.	+	.	.	MAD. end.
* <i>C. disciflora</i>	.	.	+	.	.	MAD. end.
* <i>C. distallopapillata</i>	.	+	+	.	.	EAfr.-LEM.
* <i>C. dolichodonta</i>	.	.	+	.	.	MAD. end.
* <i>C. duvignaudii</i>	.	+	+	+	.	CAfr.-LEM.
* <i>C. elegans</i>	.	+	+	.	.	Trop. Afr.
* <i>C. falcata</i>	.	.	+	.	.	Trop. AsO.
* <i>C. floccosa</i>	.	.	+	.	.	Palaeotr.
* <i>C. furcilibulata</i>	+	.	+	.	.	Trop. Afr.
* <i>C. guehoi</i>	.	.	+	+	+	MAU. end.
* <i>C. haskarliana</i>	+	.	.	+	.	Trop. Asia
* <i>C. hildebrandii</i>	.	+	+	+	.	Palaeotr.
<i>C. inflectens</i>	+	+	.	.	.	Trop. Asia
<i>C. latilobula</i>	+	+	.	.	.	Palaeotr.
* <i>C. leloutrei</i>	+	+	+	.	+	Trop. Mr.
* <i>C. lemuriana</i>	.	.	+	.	.	EAfr.-MAD
* <i>C. magillii</i>	.	+	.	.	.	COM. end.
* <i>C. malanjae</i>	EAfr.
* <i>C. marginata</i>	+	+	+	+	+	Subend.
* <i>C. mocambiquensis</i>	.	.	+	.	.	EAfr.-MAD
* <i>C. obliqua</i>	+	+	+	+	.	Pantrop.
* <i>C. onraedtii</i>	+	Subend.
* <i>C. peponiformis</i>	+	+	.	.	.	Trop. Asia
* <i>C. plagiochillana</i>	.	.	+	.	.	MAD. end.
<i>C. platyneura</i>	.	.	+	.	.	Pantrop.
* <i>C. praeruptorum</i>	.	.	+	.	.	MAD. end.
* <i>C. pteroporum</i>	.	.	+	.	.	MAD. end.
* <i>C. pusilla</i>	.	.	+	.	.	Trop. Afr.
* <i>C. raduliloba</i>	+	+	+	.	.	Trop. As-Au
* <i>C. saltuum</i>	.	.	+	.	.	MAD. end.
* <i>C. sambiroana</i>	.	.	+	.	.	MAD. end.
* <i>C. selangorensis</i>	.	.	+	.	.	MAD. end.
* <i>C. subinflata</i>	.	.	+	.	.	MAD. end.
* <i>C. takamakae</i>	.	.	.	+	.	REU. end.
* <i>C. tamatavensis</i>	.	.	+	.	.	MAD. end.

* <i>C. tanneri</i>	+	USB end.
* <i>C. tanzaniae</i>	.	+	+	.	+	+	EAfr.-MAD
* <i>C. tonkinensis</i>	.	+	+	.	.	.	Palaeotr.
* <i>C. vidaliana</i>	+	.	+	.	+	+	Palaeotr.
* <i>C. zenkeri</i>	+	.	.	.	+	+	Trop. Afr.
* <i>Colura benoistii</i>	.	+	+	.	.	.	Subend.
* <i>C. bicornis</i>	.	.	+	.	.	.	MAD end.
* <i>C. digitalis</i>	+	+	.	+	+	+	Afr.-Amer.
* <i>C. dusenii</i>	+	Trop. Afr.
* <i>C. hattoriana</i>	.	+	EAfr.-COM
<i>C. heimii</i>	.	+	+	.	+	.	Subend.
* <i>C. humbertii</i>	.	.	+	+	+	.	Subend.
<i>C. inornata</i>	.	.	+	.	.	.	MAD end.
<i>C. mauritiana</i>	+	.	MAD end.
* <i>C. obesa</i>	.	.	+	.	.	.	Subend.
<i>C. obvoluta</i>	+	.	+	.	+	.	Subend.
* <i>C. pluridentata</i>	+	Trop. AsM
<i>C. tenuicornis</i>	+	+	+	+	+	.	Pantrop.
<i>Dendrocos borbonicus</i>	+	.	.	+	+	.	EAfr.-LEM
<i>Diplasiolejeunea auriculata</i>	.	.	+	.	.	.	MAD end.
<i>D. cavifolia</i>	.	+	+	.	.	+	Pantrop.
<i>D. cobrensis</i>	.	.	+	.	.	.	Pantrop.
* <i>D. comorensis</i>	.	+	+	.	+	.	Subend.
<i>D. cornuta</i>	+	+	+	+	+	+	Trop. Afr.
<i>D. ensifera</i>	.	.	+	.	.	.	MAD end.
<i>D. hamata</i>	.	.	+	.	.	.	MAD end.
* <i>D. kraussiana</i>	.	.	+	.	.	.	EAfr.-MAD
<i>D. magnistipulata</i>	.	.	+	.	.	.	MAD end.
<i>D. subcornuta</i>	+	.	+	.	.	.	Subend.
* <i>D. symoensii</i>	.	+	+	.	.	+	EAfr.-LEM
* <i>D. utriculata</i>	.	.	+	.	.	.	MAD end.
<i>D. villaumei</i>	.	.	+	.	.	.	EAfr.-MAD
* <i>D. zakiae</i>	.	.	+	.	.	.	EAfr.-MAD
* <i>Drepanolejeunea cambouena</i>	+	+	+	.	+	+	EAfr.-MAD
* <i>D. cultrella</i>	.	+	.	.	.	+	Trop. Afr.
* <i>D. madagascariensis</i>	+	+	+	+	+	.	EAfr.-LEM
<i>D. physaefolia</i>	+	+	e	e	+	+	Palaeotr.?
* <i>D. pocsii</i>	.	+	.	.	.	+	EAfr.-COM
* <i>D. ternatensis</i>	+	Trop. Asia
* <i>D. trematodes</i>	.	+	+	.	+	.	Afr.-Amer.
<i>Frullania angulata</i>	.	+	+	+	+	+	Trop. Afr.
<i>F. apicalls</i>	+	+	+	+	+	+	Trop. Afr.
<i>F. purpurea</i>	+	.	+	.	+	.	WAfr.-LEM
<i>F. repandistipula</i>	+	+	+	+	.	.	Trop. Au
<i>F. vandenberghenii</i>	.	.	+	.	.	.	MAD end.
* <i>Harpalejeunea filicuspis</i>	+	+	Trop. AsO
<i>Lejeunea acuta</i>	.	+	.	.	.	+	EAfr.-COM
<i>L. alata</i>	+	+	+	+	+	.	Palaeotr.
<i>L. caespitosa</i>	+	+	.	.	+	+	Afr.-Amer.
<i>L. confusa</i>	.	+	Trop. Afr.
<i>L. cyathearum</i>	.	+	.	.	.	+	EAfr.-COM
<i>L. flavovirens</i>	.	+	+	+	+	+	EAfr.-LEM
<i>L. tabularis</i>	.	+	+	.	.	+	Trop. Afr.
<i>Lepidolejeunea bidentula</i>	+	.	+	.	.	.	Trop. Asia
* <i>Leptolejeunea elliptica</i>	.	+	Pantrop.
* <i>L. epiphylla</i>	+	+	.	.	+	.	Trop. Asia
* <i>L. maculata</i>	+	+	.	.	+	+	Pantrop.
<i>Metalejeunea cucullata</i>	+	+	+	.	+	.	Pantrop.
<i>Metzgeria australis</i>	.	+	.	.	.	+	Pantrop.
<i>Metzgeria consanguinea</i>	.	+	.	.	.	+	Pantrop.
<i>Microlejeunea africana</i>	+	+	+	.	.	+	Trop. Afr.
* <i>M. dispar</i>	.	.	.	+	+	.	Subend.
* <i>M. inflata</i>	.	+	+	.	.	.	Subend.
* <i>M. kamerunensis</i>	+	Trop. Afr.

* <i>M. oblongistipula</i>	+	.	.	+	.	.	Subend.
* <i>Odontolejeunea lunulata</i>	.	+	+	.	+	+	Afr.-Amer.
* <i>Otolejeunea monillata</i>	.	.	+	.	.	.	MAD end.
* <i>O. rabenorii</i>	.	.	+	.	.	.	MAD end.
<i>Plagiochila pectinata</i>	.	+	+	+	+	.	Trop. Afr.
<i>P. tenebrans</i>	.	+	+	+	.	+	Trop. Afr.
* <i>Prionolejeunea grata</i>	.	+	+	+	+	.	Trop. Afr.
<i>Pycnolejeunea ventricosa</i>	+	.	Trop. Asia
* <i>Radula flaccida</i>	.	+	.	.	.	+	Afr.-Amer.
<i>R. madagascariensis</i>	.	.	+	+	.	+	EAfr.-LEM.
* <i>R. pseudoflaccida</i>	+	USB end.
<i>R. quadrata</i>	.	+	+	+	+	.	Afr.-Amer.
* <i>R. stenocalyx</i>	.	+	+	.	+	+	Afr.-Amer.
<i>Taxilejeunea conformis</i>	+	+	+	+	+	+	Trop. Afr.
* <i>T. furcicornuta</i>	.	.	+	+	+	.	Subend.
<i>Telaranea nematodes</i>	.	+	.fr	+	.	.	Afr.-Amer.

MUSCI

	SEY	COM	MAD	REU	MAU	USB	Distribution
<i>Aerobryidium subpiligerum</i>	+	+	+	+	+	+	EAfr.-LEM
<i>Floribundaria floribunda</i>	.	+	+	.	.	+	Palaeotr.
<i>Leucoloma dichelymoides</i>	+	+	+	.	+	.	EAfr.-LEM
<i>Leucophanes angustifolium</i>	+	+	.	+	+	.	Palaeotr.
<i>Mythyridium microundulatum</i>	+	+	Subend.
<i>Syrhropodon africanum</i>	.	.	+	.	.	+	Trop. Afr.
<i>S. tixieri</i>	.	.	+	.	.	-	MAD end.

As the list shows, until now 153 species in the islands have been identified as epiphyllous, of which 117 are true epiphylls (in sense of Gradstein, 1996), marked by + in Table I, which shows their distribution in the different islands according to our present knowledge. In the right column the epiphyllous species of the continental East African Usambara Mountains are shown for comparison, based on Pócs

(1987, 1990). Finally the established distribution types are given based on their extant geographical range.

Table 2 shows the number of species belonging to these geographical distribution types on the different islands and island groups, again compared to the Usambara Mountains.

Table 2. Distribution patterns of foliicolous bryophyta in the Indian Ocean islands compared to those of the Usambara Mountains in continental East Africa

Distr. type	All isl. total	SEY	COM	MAD	REU	MAU	USB
Comoro endemic	2		2				
MAD endemic	29			29			
REU endemic	3				3		
MAU endemic	2					2	
LEM subendemic	14	6	10	13	10	10	
(USB endemic)							4)
Endemic subtotal: 50							
Tropical Africa	25	11	17	21	9	11	19
Wafr-MAD	1	.	1	1	.	1	.
Eafr-MAD	6	.	.	6	.	.	4
Eafr-COM	4	.	4	.	.	.	3
Wafr-LEM	2	2	.	2	.	1	.
Cafr-LEM	1	1	1	1	1	.	.
Eafr-LEM	11	5	9	10	6	7	8
Eafr subendemic							1
Tropical African subtotal: 50							
Palaeotr.	12	5	10	10	7	6	6
Trop. Asian	15	11	8	6	5	3	

Afr-Amer.	14	3	9	6	5	6	6
Pantropical	12	5	9	9	4	5	8
Bi- (tri-)continental subtotal: 53							
Total	153	48	80	114	50	52	59

The ratio of different geographical elements within each island or island group, and in the whole western Indian Ocean Archipelago is shown on Figure 2. As can be seen from the above data, the Seychelles are prominent among the islands by their high proportion (32%) of tropical Asian elements, of which a good number reaches its westernmost occurrence in the Seychelles (already noted by Grolle, 1978 and Pócs, 1992). The tropical African element is the highest in the Comoros (40%). Interestingly, the ratio of Afro-American disjuncts is the highest on Mauritius (12%).

Endemism (see Table 3 and Figure 2)

The rate of family and generic endemism is much higher among vascular plants than among

bryophytes. 12 families and 400 out of the 1200 higher plant genera of Madagascar are endemic (Good 1964, Takhtajan, 1986). On the other hand, there are only a few endemic genera among the Indian Ocean bryophytes and none of them are epiphylls, unless we consider the monotypic *Capillolejeunea mascarena* S.Arn. as such. This species was previously known only from Mauritius (Arnell 1965: 69) and from the Comoros (Pocs 1995: 256), on other substrates. Recently the author collected it in Northern Madagascar on a *Pandanus* leaf. In general, generic endemism is very rare among foliicolous liverworts.

The rate of species endemism on the different islands is shown in Table 3

Table 3: Rate of endemism in % among the foliicolous bryophyta in the Indian Ocean Islands, compared to that of the Usambara Moutnains.

	All isl. total	SEY	COM	MAD	REU	MAU	USB
Endemic	37.7	.	2.5	25.4	6.0	3.8	6.8
Subendemic		12.5	12.5	11.4	20.0	19.2	
Total		12.5	15.0	36.8	26.0	23.0	

Both the absolute number and the proportion of endemism is by far the highest on the large island of Madagascar (25.4% endemic and 11.4% Indian Ocean islands sub-endemic Lemurian species). This figure is, of course, also much lower than among vascular plants, of which around 80% are endemic in Madagascar (Humbert 1959). Although Reunion and

Mauritius have few strict endemics restricted to only one island (3 on Reunion and 2 on Mauritius), there are 7 Mascarenian subendemic species occurring jointly on both greater islands or some also on Rodriguez. The 12 species together comprises almost 10% of the Mascarenian epiphyllous liverwort flora

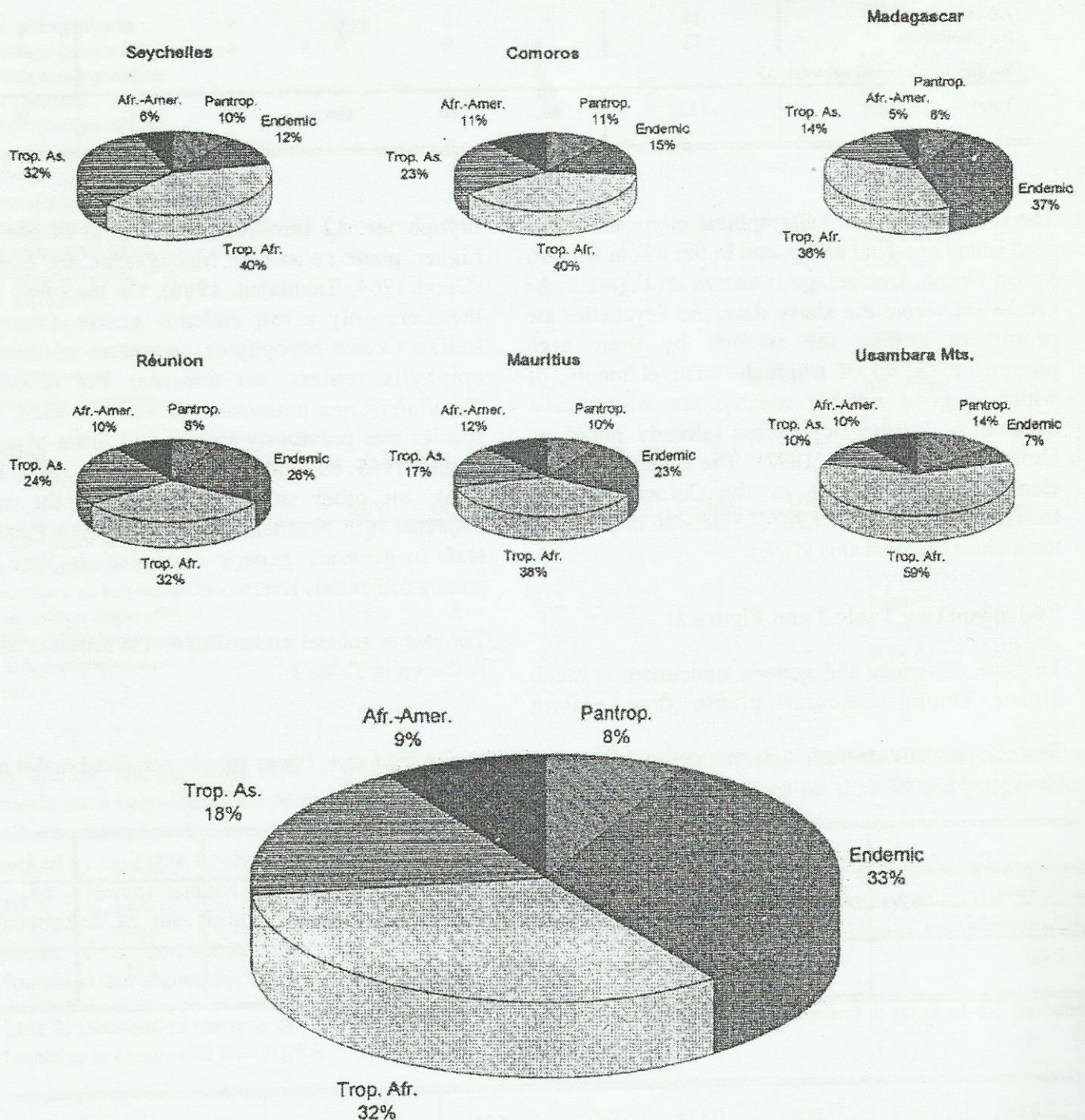


Figure 2: The percentage of different geographical distribution elements in the epiphyllous bryoflora of the islands, compared to the continental African Usambara mountains. The same proportion of all epiphyllous species in the whole archipelago is shown above.

Interestingly, the rate of endemics (see Table 3) cannot be correlated directly to the age of islands, among which Madagascar has a leading position. The Seychelles have a very low rate, although very old, and Réunion has high rate (26% with subendemics together) compared to its relatively young age. In the first case the small area is probably a limiting factor (although the islands have interesting non-epiphyllous liverwort endemics, as *Bazzania approximata* and *B. cucullata*, c.f. Grolle 1978). In the second case probably the high diversity

of habitats helped to develop such a high rate of endemism (altitudinal range from sea level to above 3,000 m, wide temperature and rainfall régime, vegetation belts offering suitable habitat for epiphylls ranging from tropical rainforest to subalpine bushes).

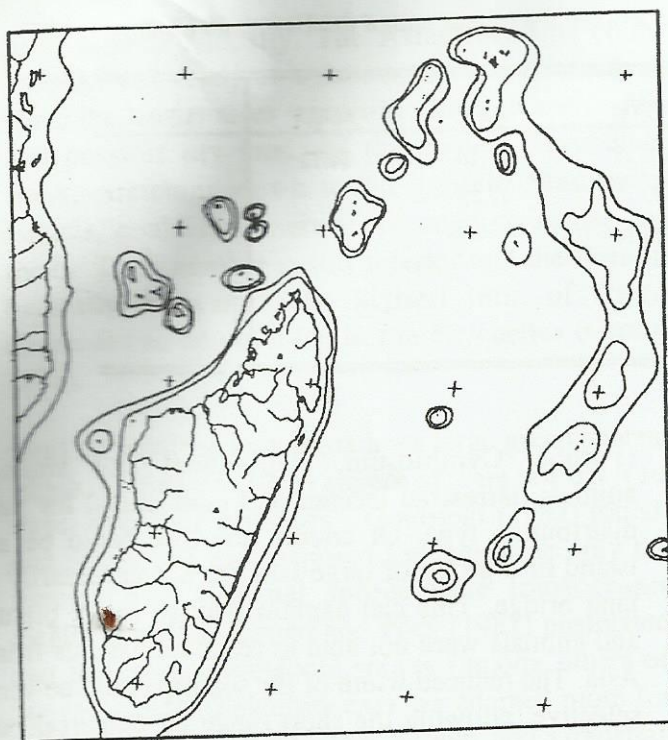


Figure 3: The ocean floor between the islands. Contours indicate 200 and 2,000 m depth. The Seychelles bank is well visible northeast from Madagascar.

Table 4: Species/genus ratio

All isl.	SEY	COM	MAD	REU	MAU	USB
4.63	1.92	3.07	4.38	3.33	4.33	2.80

The Index of Insularity proposed by Tryon (1979), based on the percent of endemism and the species/genus ratio, has shown a very different sequence to express the level of isolation. In this

case the values of insularity indices are proportional to the rate of insularity.

Table 5: Tryon Index of Insularity

All isl.	SEY	COM	MAD	REU	MAU	USB
7.28	0.52	1.14	6.03	2.10	1.11	2.79

As shown above, the rate of insularity, taking into account the species/genus ratio, is highest for the Seychelles Islands and for the continental Usambara Mountains. But using the Tryon Index of Insularity, Madagascar shows the highest value. The Usambara Mountains in continental East Africa are second in each calculation. Their moist forest areas are as well isolated in the sea of dry savanna woodland as those of the Indian Ocean islands!

This may explain, why the rate is higher than on the island of Mauritius, which has similar age and size, but much less habitat diversity. In addition, active volcanism, repeatedly creating new, uncolonized, open habitats, perhaps promotes speciation and evolution.

Insularity (see Tables 4 and 5)

The individuality of island floras can be expressed by different coefficients. The simple species/genus ratio also expresses this, being lower with increasing insularity (Gradstein & Weber 1982, Pócs 1988). It was counted 6.57 for the hepatics of Colombia (Gradstein & Weber 1982), 4.14 for Cuba (Pócs 1988) and only 1.92 for the Seychelles epiphylls and again 4.38 for Madagascar:

Affinity between the epiphyllous island floras (Table 6)

The affinity between the epiphyllous flora of the different Indian Ocean islands and the Usambara Mountains of continental East Africa was counted using Jaccard's coefficient:

Table 6: Jaccard's coefficient of foliicolous bryophyta floras between the islands and of the Usambara Mountains (%)

	SEY	COM	MAD	REU	MAU	USB
USB	21.60	37.62	26.28	21.10	24.72	
MAU	33.33	40.43	30.71	47.83		
REU	30.67	39.778	30.16			
MAD	23.66	38.57				
COM	37.63					

There is an obvious, very strong connection between the two neighbouring Mascarene islands of common origin: Réunion and Mauritius. It can be also easily understood, why the Comoro Islands in the Mozambique Channel have an affinity to the coastal Usambara Mountains almost as strong as to Madagascar on the other side. It is, however, more difficult to explain why the Comoro epiphyllous flora is more closely related to that of Réunion than to Madagascar. The link between Seychelles and Mauritius is also much closer than the affinity between these islands and Madagascar, which lies between them!

The explanation can be found only in the past, when a subcontinent stretched along the north and east side of Madagascar, indicated now by the presence of the Seychelles bank under the ocean, from which only small cays and atolls now emerge to the surface (see Figure 3). This idea was raised first by Renvoize (1979). According to him, during the time of the emergence of the Comoros and the Mascarenes these islands could have been interconnected by this land bridge. This theory cannot be proved, but the distribution of plants seems to support it. At least between the Seychelles and the Mascarenes, the sea floor is formed by this uniform sunken granitic subcontinent, which, when emergent, eliminated the sea gap between our islands and India with Sri Lanka. Geological evidence puts the time in the Jurassic or early Cretaceous, when India was separated from Madagascar and drifted away northeastwards. In the meantime the ridge of the Seychelles Bank developed between the two and emerged, serving as a stepping stone between Madagascar and India for quite a long time (Braithwaite 1984). This way, many Asian elements would have reached the archipelago, especially those which extend westwards only to this part of Africa (see many examples in Pócs 1992). There are also well known examples among vascular plant genera

(*Pothos*, *Cymbidium*, *Nepenthes*) and among animals (terrestrial leeches and land snails) for this distribution type. Of course, the link could be an island or a group of large islands, not necessarily a land bridge. This can explain why so many plants and animals were not able to reach the islands from Asia. The reduced width of the sea gap could be very selective, allowing the short range air dispersal but not land dispersal. Direct land dispersal was possible until the Cretaceous, and certainly in the Triassic (Briggs 1987), which could favour land dispersal only of archaic plant and animal groups (Keast 1973), and definitely not the epiphyllous species.

The link between the Madagascar and continental Africa, of course, was the subject of numerous investigations and much speculation. It is well documented that the separation of the continent and Madagascar started in the Jurassic, when the latter was still attached to India, this time as an island. The biological evidence, based on the distribution of 80 phanerogams common to Madagascar and Mainland Africa (Wild 1975) supported each of the three Gondwanan connections of Madagascar to the mainland proposed by geologists, but the southern position, opposite Mozambique, was favoured (Kent 1973). Pócs (1975) has shown strong bryological links with Tanzania, but on the other hand, from the very poorly known (only 103 bryophyte species) bryoflora of Mozambique more than 10% is common with Madagascar and the neighboring islands (Ochyra & Pócs 1985), while in the Usambara Mountains of northern Tanzania this element accounts for only 6.25% (Pócs 1991).

Summarizing the above, the epiphyllous bryoflora of the Indian Ocean islands might have evolved to a lesser extent from an originally local Gondwanan stock and to a greater extent through migration from the African mainland and from Asia. From these three sources a large number of endemic species has

been produced locally. The Asian migrants could have arrived partly at a time in the late Cretaceous when the land masses were still closer to each other and possible dry lands of the ancient Seychelles Bank, stretching down to the present Mascarene Islands, could have served as stepping stones for them. Their number is still inferior and the flora is basically African. The highest ratio of Asian elements can be observed in the Seychelles (Grolle 1978).

Most epiphyllous liverworts have large green spores, which, as Fulford (1951) supposed, "are not but it for travel over long distances". Gradstein (1985) found, that among the green-spored Lejeuneaceae only the species with bisexual spores have transoceanic disjunction. Van Zanten and Pócs (1981) postulated that the green, prothalloid spores (among others of the epiphyllous Lejeuneaceae) are adapted more for local dispersal. Finally, van Zanten and Gradstein (1988) could not prove this assumption experimentally.

The relatively young Comoros and Mascarenes were never connected to other land masses and the distance of their islands nearest to Africa and to Madagascar is 300 and 700 km respectively. Accordingly, we must suppose that their bryoflora had to arrive by air from a minimum distance of 300 km, from Africa, Madagascar or also from Asia, only during the past 8 million years and that the endemic stock of the islands evolved from these species. Maybe the migration from other land masses was enhanced by the above mentioned land bridge between the Seychelles and Mascarenes.

Acknowledgments

The author is indebted to Mr. András Szabó for preparing the computerized graphs. He acknowledges with thanks the financial support of this research by the Hungarian Research Fund (Grant number OTKA I/3 941).

References

- Arnell, S. (1965) Hepaticae collected by Mr. Gillis Eén in Mauritius and Réunion in 1962. *Svensk Bot. Tid.* 59: 65-84.
- Balázs, D. (1983) *Bozóttaxival Madagaszskáron*. Budapest: Gondolat. 436 pp.
- Braithwaite, C.J.R. (1984) Geology of the Seychelles. In *Biogeography and Ecology of the Seychelles Islands* (D.R. Stoddart, ed.), 17-38. The Hague: Junk.
- Briggs, J.C. (1987) *Biogeography and Plate tectonics*. Amsterdam: Elsevier, 192 pp.
- Fulford, M. (1951) Distribution patterns of the genera of leafy Hepaticae of South America. *Evolution* 5: 243-264.
- Good, R.D. (1964) *The geography of Flowering Plants*. 3rd edition. London: Longmans, 452 pp.
- Gradstein, S.R. (1985) A revision of the genus *Stictolejeunea* (Spruce) Schiffn. *Beih. Nova Hedwigia* 80: 195-220.
- Gradstein, S.R. (1996) The taxonomic diversity of epiphyllous bryophytes: introductory remarks. In *Proceedings of the IAB & IAL Symposium on Foliicolous Cryptogams*. 29 August - 2 September 1995, Eger, Hungary, in this volume.
- Gradstein, S.R., A. Lücking, M.I. Morales Z. & G. Dauphin (1994) Additions to the hepatic flora of Costa Rica. *Lindbergia* 19: 73-86.
- Gradstein, S.R. & W.A. Weber (1982) Bryogeography of the Galapagos Islands. *J. Hattori Bot. Lab.* 52: 127-152.
- Grolle, R. (1974) Eine neue *Taxilejeunea* aus Madagaskar und Réunion. *J. Bryol.* 8: 93-96.
- Grolle, R. (1975) *Haplolejeunea* aus Madagaskar - eine weitere Gattung der Tuyamaelloideae. *J. Hattori Bot. Lab.* 39: 203-210.
- Grolle, R. (1978) Die Lebermoose der Seychellen. *Wiss. Zeitschr. F.Schiller Univ. Jena, Math. Nat. R.* 27: 7-17.
- Grolle, R. (1995) The Hepaticae and Anthocerotae of the East African islands. An Annotated Catalogue. *Bryophytorum Bibliotheca* 48: 1-178.
- Grolle, R. & M. Onraedt (1974) Lebermoose aus Madagaskar und den Maskarenen (1). *Lindbergia* 2: 230-233.
- Herzog, T. (1947) Hepaticae von der Comoreninsel Johanna. *Bot. Not.* 101: 317-334.
- Humbert, H. (1959) Origines présumées et affinités de la flore de Madagascar. *Mém. Inst. Sci. Madagascar, Ser. B, Biol. Vég.* 9: 149-187.
- Jovet-Ast, S. (1956) Deux *Colura* nouveaux de Madagascar. *Rev. Bryol. Lichénol.* 25: 272-276.
- Jovet-Ast, S. (1958) Localités nouvelles de diverses espèces du genre *Colura*. *Rev. Bryol. Lichenol.* 27: 19-23.
- Jovet-Ast, S. (1959) Un *Microlejeunea* nouveau de l'île de la Réunion. *Rev. Bryol. Lichénol.* 27: 191-194.
- Jovet-Ast, S. (1983) *Colura* nouveaux d'origines divers (Hépatiques, Lejeuneacées). *Cryptogamie, Bryol. Lichenol.* 4: 205-216.
- Kent, P.E. (1973) East African evidence of the palaeoposition of Madagascar. In *Implications of Continental Drift to the Earth Sciences* (Darling D.H. and S.K. Runcorn, eds.), 2: 873-877.
- Ochyra, R. & Pócs, T. (1985) East African Bryophytes, XI. Dr. L. Péntek's collection from Mozambique. *Abstracta Botanica* 9, Suppl. 2: 63-86.
- Onraedt, M. (1977) Bryophytes des Îles mascareno-malgaches et Seychelles III. Hepaticae: *Bazzania*. *Bull. Jard. Bot. Nat. Belg.* 47: 139-144.
- Pócs, T. (1975) Affinities between the bryoflora of East Africa and Madagascar. In *Origines des flores africaines et malgaches*. *Nature, speciation*. Miège, J. & A. Stork, eds.),

- Comp.-rend. de la VIII^e réunion de l'AETFAT, I. Boissiera 24a: 125-128.
- Pócs, T. (1984) Present knowledge on *Aphanolejeunea* Evans. J. Hattori Bot. Lab. 55: 307-313.
- Pócs, T. (1988): Biogeography of the Cuban Bryophyte Flora. Taxon 37: 615-621.
- Pócs, T. (1991) Geography and ecology of Usamabara's bryophytes. In Research for Conservation of Tanzanian Catchment Forests. (Hedberg, I. & E. Persson, eds.) Proceedings from a workshop held in Morogoro, Tanzania, March 13-17, 1989 71-85. Uppsala: Univ. of Uppsala.
- Pócs, T. (1992) Correlation between the tropical African and Asian bryofloras. II. In Proceedings of the Congress of East Asiatic Bryology (Koponen T. and J. Hyvönen, eds.), Helsinki, August 12-19, 1990 - Bryobrothera 1: 35-47.
- Pócs, T. (1993) New or little known epiphyllous liverworts, IV. Two new *Cololejeuneoideae* from the Comoro Archipelago. J. Hattori Bot. Lab. 74: 45-57.
- Pócs, T. (1995) East African bryophytes, XIV. Hepaticae from the Indian Ocean Islands. Fragm. Flor. Geobot. 40: 251-277.
- Pócs, T. (1996) Epiphyllous liverwort diversity at worldwide level and its threat and conservation. Annales Inst. Biol. Univ. Nac. Autón. Mexico, Ser. Bot. 67: 109-127
- Renvoize, S.A. (1979) The origins of Indian Ocean island floras. In Plants and Islands. (D. Bramwell, ed.), 107-129. London: Academic Press.
- Tixier, P. (1976) Espèces nouvelles malgaches du genre *Diplasiolejeunea* (Spruce) Schiffn. (Hepaticae). Lindbergia 4: 117-125.
- Tixier, P. (1977) La spéciation lémurienne et les Lejeuneacées. Le cas du genre *Diplasiolejeunea*. Bryophytorum Bibliotheca, 4. Cramer, Vaduz 13: 622-645.
- Tixier, P. (1979a) La famille des Cololejeuneoideae (Grolle) dans l'Océan Indien Occidental. Bull. Acad. Malgache 55: 173-247.
- Tixier, P. (1979b) Nouvelles espèces Malgaches de *Diplasiolejeunea* (Diplasiae). II. Rev. Bryol. Lichenol. 45: 209-226.
- Tixier, P. (1984) Contribution à l'étude du genre *Diplasiolejeunea* (Spruce) Schiffner. 4. La section *Villaumeae* P.Tx. (Subgenus *Diplasiolejeunea*). Acta Bot. Hungarica 30: 11-26.
- Tixier, P. (1985) Contribution à la Connaissance des Cololejeuneoideae. Bryophytorum Bibliotheca, J. Cramer, Vaduz, 27: 439 pp.
- Tryon, R. (1979) Biogeography of the Antillean fern flora. In Plants and Islands. (D. Bramwell, ed.), 55-69. London: Academic Press.
- Vesey-Fitzgerald, D. (1942) Further studies of the vegetation on islands in the Indian Ocean. J. Ecol. 30: 1-16.
- Wild, H. (1975) Phytogeography and the Gondwanaland position of Madagascar. In Origines des flores africaines et malgaches. Nature, speciation. Miège, J. & A. Stork, eds.), Comp.-rend. de la VIII^e réunion de l'AETFAT, I. Boissiera 24a: 107-117.
- Zanten, B.O. & S.R. Gradstein (1988) Experimental dispersal geography of neotropical liverworts. Beih. Nova Hedwigia 90: 41-94.
- Zanten, B.O. & T. Pócs (1981) Distribution and dispersal of bryophytes. In Advances in Bryology (Schultze-Motel, W. ed.), 1: 479-562. Vaduz: J. Cramer.