

EPIPHYLLOUS LIVERWORT DIVERSITY AT WORLDWIDE LEVEL AND ITS THREAT AND CONSERVATION

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RESUMEN

Se preparó un banco de datos de 1000 especies de hepáticas epifilas que incluyen 389 especies de *Cololejeunea*, 114 de *Ceratolejeunea*, 98 de *Drepanolejeunea*, 76 de *Colura*, 68 de *Diplasiolejeunea*, 59 de *Prionolejeunea*, 54 de *Aphanolejeunea*, 48 de *Leptolejeunea*, 34 de *Microlejeunea*, 13 de *Radula* y otros 12 géneros con menos de 10 especies. Se registró la distribución de estos 22 géneros en cada una de las 21 regiones florísticas donde ocurren epifilas. Entre los continentes, Asia con 504 especies (incluyendo la región florística del Archipiélago Malesiano con 224 especies), fue la más rica; América con 375 especies (incluyendo las Antillas con 178) fueron los siguientes. Las hepáticas epifilas crecen principalmente en los bosques lluviosos tropicales y subtropicales. Cualquier impacto sobre la estructura del dosel u otras capas del hábitat del bosque causa serio empobrecimiento o pérdida total de las comunidades folícolas por lo que su conservación sólo puede lograrse a través de la protección rigurosa de los bosques.

Palabras clave: epifilas, Hepaticae, bosques lluviosos, diversidad, conservación.

ABSTRACT

A data bank for 1000 epiphyllous liverwort species includes 389 species of *Cololejeunea*, 114 of *Ceratolejeunea*, 98 of *Drepanolejeunea*, 76 of *Colura*, 68 of *Diplasiolejeunea*, 59 of *Prionolejeunea*, 54 of *Aphanolejeunea*, 48 of *Leptolejeunea*, 34 of *Microlejeunea* and 13 of *Radula* and 12 other genera with less than 10 species each. The distribution of epiphyllous species of these 22 genera was recorded within 21 floristic regions (Takhtajan, 1986; modified) where epiphylls occur. Among the continents Asia, with 504 species (including the floristic region of the Malesian Archipelago with 224 species) proved to be the richest overall. The Americas with 375 species (including the Antilles with 178 species) are the second. Epiphylls are found primarily in the tropical and subtropical rainforests. Any impact on the structure of the canopy or other layers of the forest

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habitat causes serious impoverishment or total loss to these foliicolous communities, therefore their conservation is possible only through strict protection of concerned rainforest areas.

Key words: epiphylls, Hepaticae, rainforests, diversity, conservation.

INTRODUCTION

The phyllosphaere (in the sense of Ruinen, 1961) is a special environment where in the temperate regions only a poor community with limited number of fungi and algae can occur, while among the ever-moist and warm conditions of the tropical and subtropical rainforests very rich foliicolous communities develop. Since the preliminary studies of Massart (1898) and Busse (1905) various studies have been devoted to their ecology. The most important component of these communities are the epiphyllous Hepaticae, mainly members of the family *Lejeuneaceae*. Along with the liverworts, mosses, foliicolous lichens, algae and fungi may also occur. Outside the tropics and subtropics, bryophyte communities inhabit living leaves only when superoceanic conditions prevail, like in the Macaronesian islands (Sjögren, 1975, 1978), in British Columbia (Vitt *et al.*, 1973), in the Appalachians (Schuster, 1959), and at the foot of Caucasus Mountains (Pócs, 1982).

The diversity of epiphyllous liverworts appears to be correlated with the diversity of the whole of the rainforest community. The author has tried to establish a data bank of the epiphyllous Hepaticae of the World, keeping all records on their occurrence in the main floristic regions. The selection of the taxa included in the data bank is somewhat arbitrary for two reasons. First, it is very difficult to draw limits between epiphyllous and non epiphyllous species. One may distinguish obligate and facultative epiphylls; the first group would include those taxa which occur exclusively on living leaves, while the second group would include those which occur on different substrates, including leaves. There are genera (*e.g.*, *Leptolejeunea*) where all species seem to be restricted to living leaf substrates. The author has, however, observed *Leptolejeunea* species on smooth bark, bamboo stems, on iron railings in a national park and even on a discarded plastic Coca-Cola bottle. Both Olarinmoye (1975) and Schuster (1980) observed the occurrence of *Radula flaccida*, considered to be an obligate epiphyllous species, on bark in different continents. Jones, according to Richards (1984), doubts whether any hepatics are exclusively epiphyllous.

There are also other genera, such as *Aphanolejeunea*, *Cololejeunea*, *Cyclolejeunea*, *Odontolejeunea*, *Prionolejeunea*, and *Rhaphidolejeunea*, where almost all species are known to occur on leaves. In *Drepanolejeunea*, most species inhabit leaves but certain taxonomic groups are corticolous (Bischler, 1964). Again most species of certain genera (*e.g.*, *Diplasiolejeunea* and *Colura*) can be considered epiphyllous, but many of them can occur also on small twigs. A few species of these genera, especially those from high montane habitats, were never observed on leaves but seem

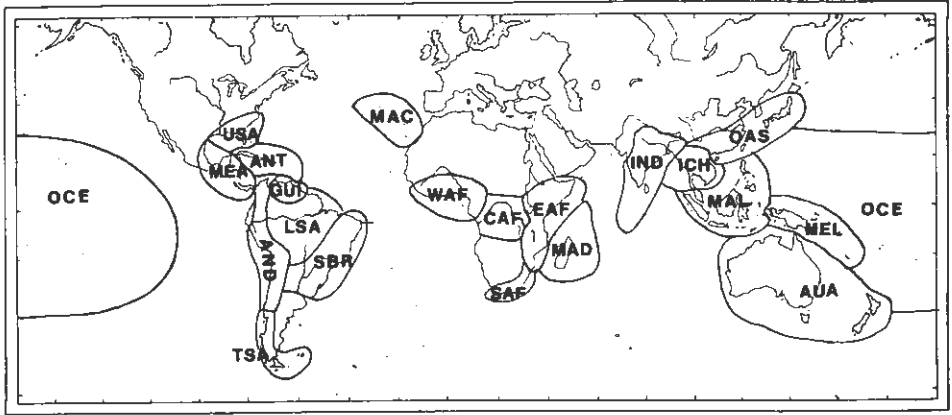


Fig. 1A. Floristic regions where epiphylls occur. USA: The SE part of United States. MEA: Mesoamerica from Mexico to Panama. ANT: The Antilles. GUI: The Guyanas, including the Venezuelan and Brazilian parts of Guyana Highlands. LSA: Amazonia and other lowland parts of South America, such as Choco and the Orinoco basin. SBR: The southeastern highlands of Brazil, with Paraguay and the Province Misiones in Argentina. AND: The Andes. TSA: Temperate South America. MAC: Macaronesia (excluding Cape Verde Islands). WAF: West Africa from Guinea to the Congo. CAF: Central Africa including Zaire, Rwanda and Burundi. EAF: East Africa from Ethiopia to Mozambique. SAF: South Africa. MAD: Madagascar and the Seychelles, Comoro and Mascarene Islands. IND: India with the Himalayas, Khasia Hills (but excluding Andaman and Nicobar Islands) and lowland Bangladesh and Sri Lanka. OAS: East Asia including China, Taiwan, South Korea and Southern Japan with the Ryukyu Islands. ICH: Indochina from the Chittagong Hills of Bangladesh to Vietnam. MAL: The Malasian Archipelago including the Andaman and Nicobar Islands and the Malay Peninsula but excluding West Irian. MEL: Melanesia, including the whole New Guinea, New Britain, the Bismarck and Solomon Islands, New Hebrides and New Caledonia. AUA: Australasia, including Australia, Tasmania, New Zealand and the neighbouring islands. OCE: Oceania, the Pacific from Volcano and the Carolines to Hawaiian Islands and from Fiji to Easter Islands.

to inhabit exclusively thin twigs or sometimes the bark of thicker tree trunks (e.g., *Diplasiolejeunea pauckertii*, *D. columbica*, *Colura ornithocephala*, and *C. kilimanjarica*). With other genera, the majority of species is mostly epiphyllous but can occur on other substrates as well. They are usually very constant members of the epiphyllous communities, like species of *Ceratolejeunea* or *Microlejeunea*.

With the exception of the obviously non epiphyllous species, those members of genera of the above types are considered to be "typically epiphyllous", (a term suggested by S.R.Gradstein, 1996), rather than "obligately epiphyllous". The present study deals exclusively with typical epiphylls.

Practically all well known adaptations to the foliicolous life form can be observed in these genera, so nicely described by Goebel (1888, 1889), Bischler

(1968) and Winkler (1970). These species are pioneers in the colonization of leaves (Winkler, 1967; Pócs, 1978).

Obviously, the transition between this and the next group is continuous. There are genera, such as *Caudalejeunea*, *Cheilolejeunea*, *Harpalejeunea*, *Lepidolejeunea*, *Lopholejeunea*, *Marchesinia*, *Pycnolejeunea*, *Stictolejeunea* and *Tuyamaella*, which occur at almost equal rates on leaves and on bark or on rocks or even on decaying wood. Then, there are genera (like *Lejeunea*, *Frullania*, and *Metzgeria*), of which the majority of species are not epiphyllous but certain species are very common on leaves like *L. eckloniana*, *L. flava*, and *Frullania apiculata*. Only a few species of these genera seem to be exclusively epiphyllous, e.g., *Lejeunea dimorpha*, *Frullania epiphylla*, and *Metzgeria epiphylla*. Members of such genera were not included in the present study; in general, they should be considered facultative epiphylls.

In very wet conditions of the superhumid rainforests, like in Choco, North Madagascar or in New Guinea and many other places with rainfall more than 3000 mm/year, almost any liverwort (from *Acromastigum* to *Zoopsis*) and many mosses can occur on living leaves. These species, which in other cases do not occur on leaves, might be classified as accidental epiphylls.

The second reason why my selection of epiphyllous taxa is a bit arbitrary, is that the level of revision among the genera is very different. This relates not only to the time that a particular group was revised, but also the species concept of the author of a revision. There are epiphyllous genera with good taxonomic treatments, such as *Colura*, *Drepanolejeunea*, *Leptolejeunea*, *Odontolejeunea* or *Rhaphidolejeunea*, which were revised very recently. Then there are genera, such as *Prionolejeunea*, where no revision has been made since Spruce (1885), Stephani (1898-1924) or Evans (1902-1912). In the latter case we can speak only about "described species". *Cyclolejeunea* was omitted from the calculations since most of the 33 described species surely belong to other genera, and the rest, distinguished by minute characters, probably represents a much lower number of species. A recent treatment by Grolle (1984) gives only generic limits, descriptions of the subgenera and treats only the Cuban species.

Thus the 1000 species selected for the present treatment is based upon the above considerations. Previous calculations, based on a much lower number of species, has been published earlier (Pócs, 1978), but no attempt has been made yet to investigate the distribution of nearly all typically epiphyllous liverwort species. Such an investigation, it is hoped, will reveal the rate of epiphyllous diversity in each genus and within each geographical (floristic) unit which will help conservation work since epiphyllous biodiversity is very different from area to area. An additional task will be the investigation of the epiphyllous vegetation diversity from place to place, since according to our experience (Pócs and Tóthmérész, 1996), even the rate of degradation is well reflected by the average number of species per leaf.

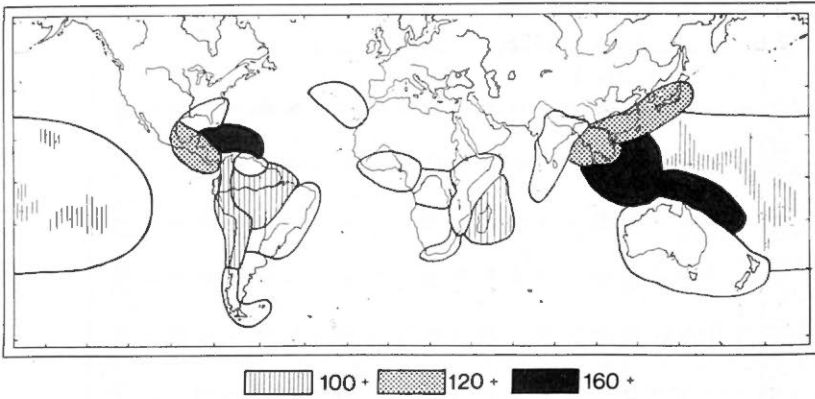


Fig. 1B. Floristic regions with epiphyllous species number higher than 100, 120 and 160.

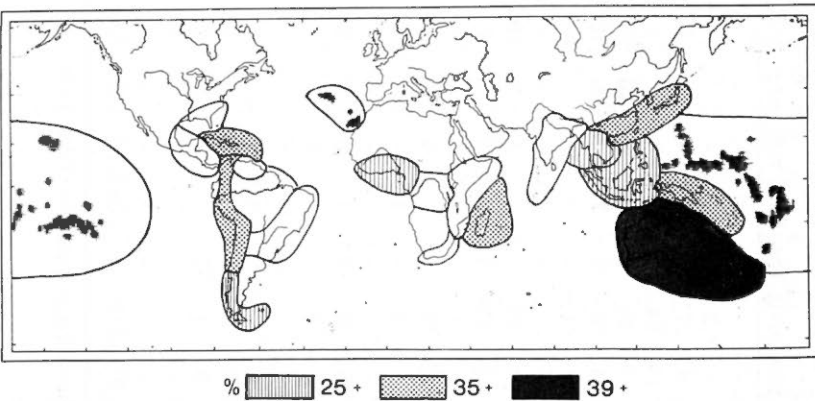


Fig. 1C. Floristic regions with rate of endemism higher than 25%, 35% and 39% compared to the total number of epiphylls.

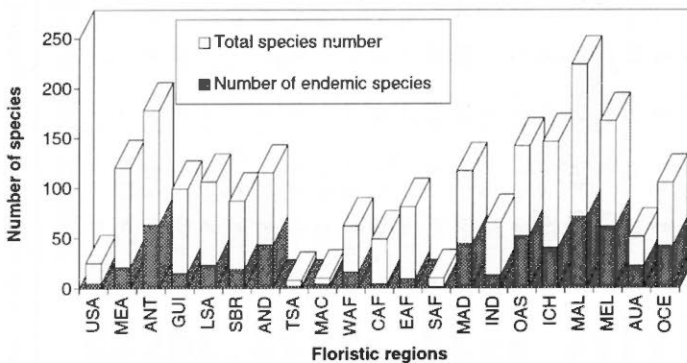


Fig. 2. Epiphyllous species richness in the 21 floristic regions of the world.

Table 1. Total number of epiphyllous species in different floristic regions of the world

No. of spec.	No. of spec.														Total:							
	USA	MEA	ANT	GUI	LSA	SBR	AND	TSA	MAC	WAF	CAF	EAF	SAF	MAD		IND	OAS	ICH	MAL	MEL	AUA	OCE
<i>Acantholejeunea</i>	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-
<i>Anoplolejeunea</i>	3	1	1	-	2	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Aphanolejeunea</i>	54	6	14	18	5	6	7	2	3	4	5	6	1	4	1	4	3	4	7	3	-	-
<i>Ceratolejeunea</i>	114	2	22	33	23	25	16	34	-	8	2	1	-	4	-	3	1	12	6	1	10	-
<i>Cololejeunea</i>	389	6	18	12	9	16	17	10	1	2	25	18	36	4	55	35	80	92	101	69	27	52
<i>Colura</i>	76	-	3	9	7	6	6	6	1	1	4	4	10	2	13	3	6	16	28	23	10	5
<i>Cyrtolejeunea</i>	4	-	3	3	2	4	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cystolejeunea</i>	1	-	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Diplasiolejeunea</i>	68	1	14	29	10	4	7	10	-	5	7	10	-	18	-	3	3	5	2	3	2	-
<i>Drepanolejeunea</i>	98	4	18	18	11	9	11	14	1	2	4	4	7	2	7	8	18	9	31	25	5	17
<i>Echinoclea</i>	1	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Leptolejeunea</i>	48	1	6	6	7	9	6	2	-	4	3	4	-	4	9	15	10	22	12	1	10	-
<i>Macrolejeunea</i>	7	-	-	2	-	-	5	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Metzgeriopsis</i>	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-
<i>Microlejeunea</i>	34	4	9	5	7	7	3	8	2	1	3	2	2	1	6	3	4	3	3	2	1	4
<i>Odonolejeunea</i>	3	-	3	2	3	2	1	3	-	1	1	1	1	-	1	-	-	-	-	-	-	-
<i>Otolejeunea</i>	8	-	-	-	-	1	-	-	-	-	-	-	-	2	-	-	-	1	1	3	-	-
<i>Papillolejeunea*</i>	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
<i>Prionolejeunea</i>	59	-	4	35	11	10	7	11	-	2	1	1	1	1	1	-	-	1	1	1	-	1
<i>Radula</i> sect. <i>Epiph.</i>	13	1	4	4	2	3	3	1	1	2	2	3	-	2	4	5	6	6	5	-	3	-
<i>Rhaphidolejeunea</i>	9	-	-	-	1	1	-	-	-	-	-	-	-	-	1	3	3	3	2	-	-	-
<i>Stenolejeunea</i>	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	5	5	-	1	-
Total:	1000	25	120	178	99	106	87	115	8	10	62	49	81	10	117	64	142	147	224	167	51	105

* The generic name will be validly published in a forthcoming publication (Pócs, 1996).

Table 2. Number of endemic species, which do not occur outside the region studied

En- de- mic taxa of	USA	MEA	ANT	GUI	LSA	SBR	AND	TSA	MAC	WAF	CAF	EAF	SAF	MAD	IND	OAS	ICH	MAL	MEL	AUA	OCE		
<i>Acantholejeunea</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Anoplolejeunea</i>	2	3	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Aphanolejeunea</i>	21	54	1	4	1	2	2	1	2	2	1	1	1	2	1	2	2	2	3	1	-	-	
<i>Ceratolejeunea</i>	68	114	-	6	11	4	3	2	21	-	5	-	-	-	-	1	-	7	2	-	6	-	
<i>Cololejeunea</i>	255	389	2	10	5	3	10	10	6	-	1	4	1	5	1	20	9	34	28	39	32	12	24
<i>Colura</i>	39	76	-	-	1	-	3	-	1	-	-	-	3	-	6	-	1	7	6	6	5	-	-
<i>Cyrtolejeunea</i>	2	4	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cystolejeunea</i>	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Diplasiolejeunea</i>	40	68	-	2	16	3	-	2	2	-	-	-	-	11	-	-	-	1	-	3	-	-	-
<i>Drepanolejeunea</i>	40	98	2	1	3	-	-	-	3	2	-	-	-	-	1	4	-	7	8	1	7	-	-
<i>Echinocolea</i>	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Leptolejeunea</i>	22	48	-	-	-	-	1	1	-	-	-	-	-	-	1	8	1	7	1	-	-	2	-
<i>Macrolejeunea</i>	6	7	-	-	1	-	-	4	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Metzgeriopsis</i>	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Microlejeunea</i>	13	34	-	-	-	-	1	-	-	1	-	-	-	4	1	2	-	-	1	-	3	-	-
<i>Odontolejeunea</i>	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Otolejeunea</i>	7	8	-	-	-	-	1	-	-	-	-	-	-	2	-	-	1	1	2	-	-	-	-
<i>Papillolejeunea</i>	3	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
<i>Prionolejeunea</i>	37	59	-	1	20	3	2	1	6	1	-	1	-	-	-	-	-	-	1	1	-	-	-
<i>Radula</i> sect. <i>Epiph.</i>	3	13	-	-	1	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
<i>Rhaphidolejeunea</i>	4	9	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	1	-	-	-
<i>Stereolejeunea</i>	1	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Number of endemic species:	5	21	63	15	23	19	43	2	4	16	4	9	1	44	13	52	40	71	61	92	42	-	-
out of the total:	25	120	178	99	106	87	115	8	10	62	49	81	10	117	64	142	147	224	167	51	105	-	-
Percent of endemics (%)	20.0	17.5	35.4	15.1	21.7	21.8	37.4	25.0	40.0	25.8	8.2	11.1	10.0	37.6	20.0	36.6	27.2	31.7	36.5	43.1	40.0	-	-

MATERIAL AND METHODS

In order to achieve the above goals, a data bank was established, based upon literature records from all available taxonomic revisions, checklists or smaller publications and likewise included my unpublished data. I tried to recognize on the basis of literature, all synonyms. Then I tried to identify the distribution of the species in the 21 floristic regions where epiphylls occur (see Fig. 1A). These floristic regions were based to some extent on Takhtajan (1986), but were strongly modified for bryological and for practical reasons.

I am sure that the data bank produced in this way is far from complete, especially because of the unrevised groups. A further task will be to include the epiphyllous members of the otherwise primarily non epiphyllous genera. At any rate, the large amount of data collected up to the present has made it possible to count the number of typically epiphyllous species by continents and in each floristic region, and to calculate the rate of endemism in each region, according to genus, to show the division of species in the different genera according to continents, and in each floristic region. The above tabulations clearly show the geographic regions with the highest epiphyllous diversity and call attention to possible centres of evolution. Finally, an attempt is made to summarize the long field experiences of the author in regard to the different threats to the epiphyllous vegetation and to propose possible means for their conservation.

DISCUSSION

Richness of the epiphyllous flora

The richness of the epiphyllous hepatic flora in different floristic regions is summarized in Table 1 and in figure 1B and 2. High species diversity occur in all continents, but at different levels. As it is shown, the overall highest epiphyllous diversity among the floristic regions appears in Malesia (224 species), the second highest in the Antilles (178) and the third in Melanesia (167 species). The high epiphyllous diversity of the last area is discussed by Piippo (1994). They represent at the same time the highest figures within their continents, while in Africa, Madagascar with the neighboring Indian Ocean islands is first. All these centres with high epiphyllous diversity are archipelagos! On the larger land masses of the continents only the Mesoamerican range, Indochina and the Far East have, to some extent, comparable richness. This seems to underline the importance of island isolation by epiphylls, and, at the same time, their general inability for long range air dispersal, although there are some pantropical species. Part of these widespread taxa is somewhat "weedy", indicating the probability for long range, secondary dispersal, as in the case of *Cololejeunea cardiocarpa*.

The richness of major epiphyllous genera within different floristic regions is

Table 3. Number of epiphyllous species according to genera in the different continents

	Americas	Africa	Asia + Australasia +Oceania
<i>Acantholejeunea</i>	-	-	1
<i>Anoplolejeunea</i>	3	-	1
<i>Aphanolejeunea</i>	29	10	15
<i>Ceratolejeunea</i>	85	13	16
<i>Cololejeunea</i>	62	79	275
<i>Colura</i>	16	19	48
<i>Cyrtolejeunea</i>	4	-	-
<i>Cystolejeunea</i>	1	-	-
<i>Diplasiolejeunea</i>	41	23	10
<i>Drepanolejeunea</i>	31	13	57
<i>Echinocolea</i>	1	-	-
<i>Leptolejeunea</i>	12	5	37
<i>Macrolejeunea</i>	7	-	-
<i>Metzgeriopsis</i>	-	-	1
<i>Microlejeunea</i>	17	8	11
<i>Odontolejeunea</i>	3	1	0
<i>Otolejeunea</i>	1	2	5
<i>Papillolejeunea</i>	-	-	3
<i>Prionolejeunea</i>	55	2	3
<i>Radula</i> Sect. <i>Epiphyllae</i>	6	3	7
<i>Rhaphidolejeunea</i>	1	-	8
<i>Stenolejeunea</i>	-	-	6
Total	375	178	504

shown in figure 3. The centers of diversity are different for different genera, although many times these coincide with one or two of the above discussed overall regional centers. For example, *Diplasiolejeunea* shows an obvious double peak in the Antilles and in Madagascar; *Ceratolejeunea* has a double peak in the Antilles and in the Andes, while *Cololejeunea* species have the highest diversity in Malesia and in the adjoining regions.

The richness of the epiphyllous flora tabulated according to continents or continental groups is shown in Table 3. Again, Asia is the richest with 504 species, followed by 375 species in the Neotropics. Africa is the poorest with only 178 species. It is interesting to note that both Asia and the Americas have four endemic epiphyllous genera

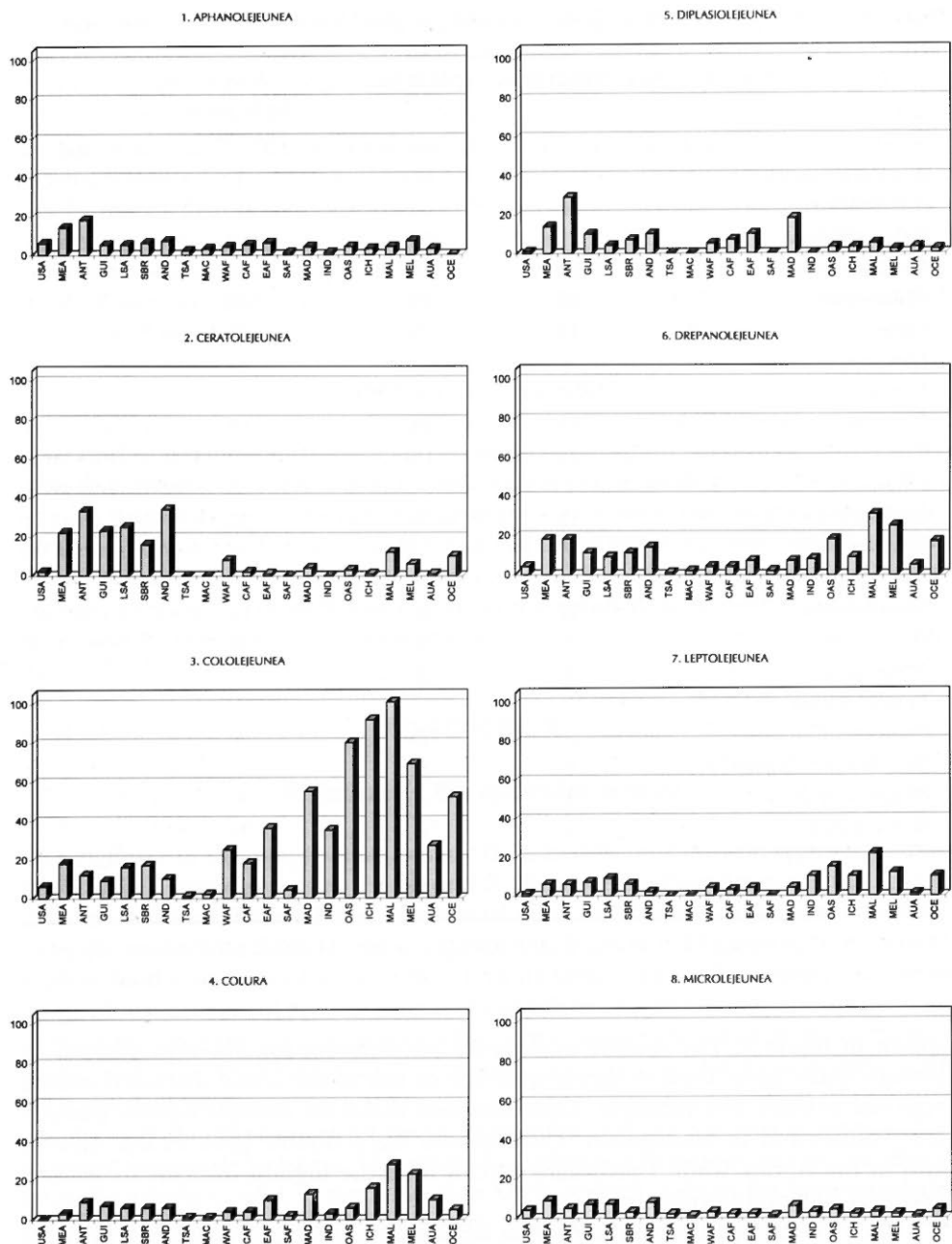


Fig. 3. Species number of the eight major epiphyllous genera within the different floristic regions.

each while Africa has none. The endemic Lejeuneaceae genera of Madagascar and the Mascarene islands, *Capillolejeunea* and *Haplolejeunea*, are not epiphyllous.

The division of the most important epiphyllous genera, according to their number of species on the different continents, is shown in figures 4 and 5. All of the larger genera are represented on each continent, but the ratio of the species per continent is very different. *Colura*, *Cololejeunea*, *Drepanolejeunea* and *Leptolejeunea* have an overwhelmingly Asian majority, while the other "big four" have clearly American domination. This ratio is reflected in the composition of epiphyllous communities too, which in the different continents, are dominated by the species of the concerned genera. Africa is transitional and can be characterized by a relatively large number of both *Diplasiolejeunea* and *Cololejeunea* species.

The rate of endemism

The rate of endemism among epiphylls shows a pattern quite different from that of species richness. It must be taken into account that bryophytes normally show a much lower rate of endemism than the phanerogam flora of the same area (Gradstein and Pócs, 1989). On the other hand, epiphylls have usually a higher rate of endemism, than the rest of the bryophytes. The number of endemic species within each floristic region, according to genera, is shown on Table 2, figure 1C and in figures 6-8. Regions which are not especially rich in species like West Africa, Australasia, Macaronesia and Oceania, may have a high rate of species endemism - as high as 26, 43 and 40-40%, respectively. It is difficult to explain why the highest rate of endemism occurs in Australasia although the total number of species is low. The reason may be partly due to the fact that a number of species with a southern temperate, Gondwanian origin occur there (*cf.* Thiers, 1990) which do not penetrate further north, and that Australia and New Zealand, as quite intact and isolated pieces of former Gondwanaland, could develop their indigenous flora also in the field of epiphylls (similarly to the phanerogams). The second highest rate of endemism seems to occur in the Macaronesian and in the Oceanian archipelagoes where insular speciation and isolation was obviously promoted by the large distance between island groups compared to their small size of land area, as shown by Miller and Whittier (1990). Mountain ranges, like the Andes, are also important regional centers of endemism (see also Gradstein *et al.*, 1989). Schuster (1990) explains the diversity and richness of the hepatic flora in this area by tectonic instability that has occurred here in the past. Another area with a relatively high rate of endemism is the Far East including South China, South Korea, southern Japan and all islands adjoining these countries. Their epiphyllous flora is fairly well known and several accounts have been published (*e.g.*, Horikawa, 1932; Chen and Wu, 1964; Luo 1990). This richness in endemics is probably the result of very dissected land surfaces with a geologically different age.

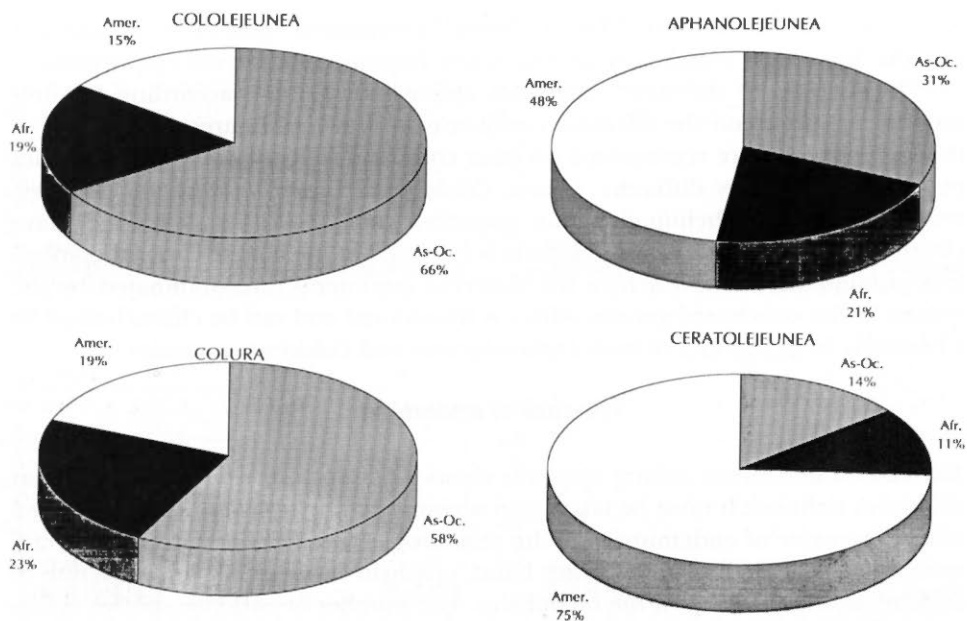


Fig. 4. The division of species of the eight major epiphyllous genera among the continents, I.

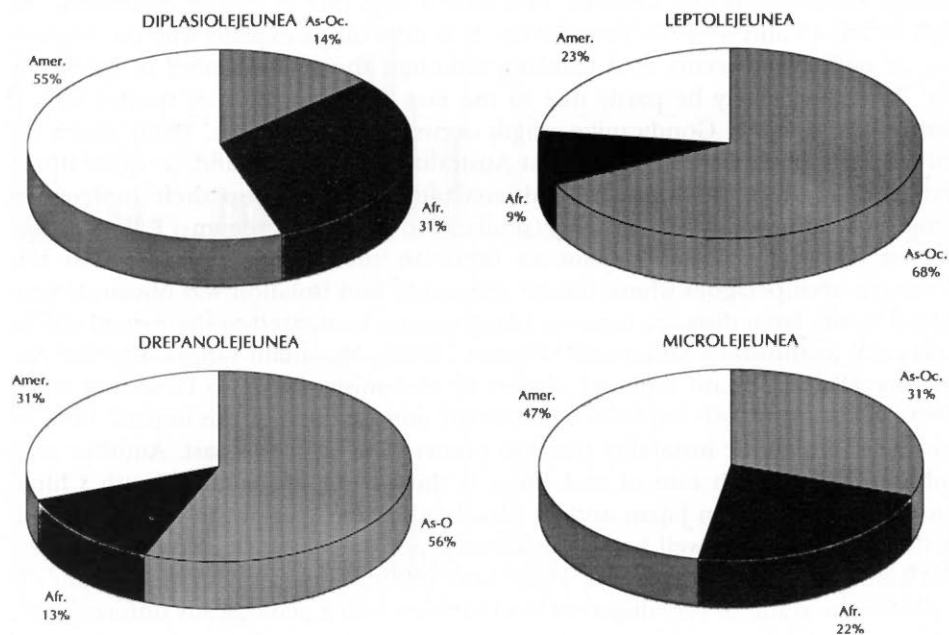


Fig. 5. The division of species of the eight major epiphyllous genera among the continents, II.

Threats on the epiphyllous flora and vegetation

Obviously, total deforestation and depletion of tropical rainforests, converting them into more or less degraded agricultural land or pasture, is the greatest threat to the epiphyllous flora and vegetation bound to the rainforest biome. According to Reid (1992) the rate of closed forest loss in all tropics is more than 10 million hectares per year which means 1% annually and, according to the estimates this means 4-8% loss of all larger forest species by the end of this century and up to 20% by 2040. Other estimates (Raven, 1987, 1988) predict that the situation is even worse whereby 25% of tropical forest plant species will be lost by the year 2015, with a rate of 2000 species/year.

Epiphylls are more vulnerable than the majority of tropical forest plants, including other bryophytes. Corticolous or saxicolous bryophytes might survive in small niches even after the destruction of the forest cover. No other bryophyte group is so dependent on the microclimate created by the vegetation, as are the epiphylls. Epiphyllous liverworts, at least for the most part, are considered shade epiphytes in the sense of Richards (1983, 1984). Shade epiphytes, with high air moisture requirements, belong to the most threatened bryophyte components of tropical rainforests (see Hyvönen *et al.*, 1987; Gradstein, 1992a, 1992b, 1994) which partly or totally disappear due to human influence. Epiphylls are usually restricted to special microclimate pockets in the lower vegetation stories of the rainforest (Richards, 1984; Wu *et al.*, 1987). Only in cloud forests or in a very wet type of other rainforests do epiphylls commonly occur even in the canopy.

According to recent field studies in the Seychelles (Pócs and Tóthmérész, 1996), the appearance of introduced species (*e.g.* cinnamon) in the canopy can highly decrease the species number per leaf and change the composition of the epiphyllous communities. The invasion by exotics or the replacement of the original canopy by plantation trees usually means the total loss of the epiphyllous flora. Parts of the rainforests of the East Usambara Mountains (Tanzania) are invaded by the introduced *Maesopsis eminii* (tall Rhamnaceae tree, native to Uganda). The seeds of this species are easily dispersed by birds (hornbills), and the quickly spreading tree in many locations has partly or fully replaced the original canopy. Due to its effect on microclimate the otherwise rich epiphyllous vegetation has completely disappeared, together with other shade epiphytes such as filmy ferns. Only the sun epiphytes persisted, descending to the lower strata and occupying even the trunk bases of *Maesopsis* trees (Pócs, 1989). On the southern slope of the Kilimanjaro Mountains only 10% of the former forest bryoflora has survived under the broadleaved plantation trees (Pócs *in* Gradstein, 1992a). In narrow-leaved plantation forests, such as exotic *Cupressus*, *Pinus*, *Casuarina*, and in *Eucalyptus* plantations, a complete change of the microclimate (light and moisture regime) takes place, accompanied by changed soil conditions of the original rainforest. There is no longer a chance for any epiphyllous liverworts or for other shade epiphytes to survive. Hyvönen *et al.* (1987) observed the massive appearance of

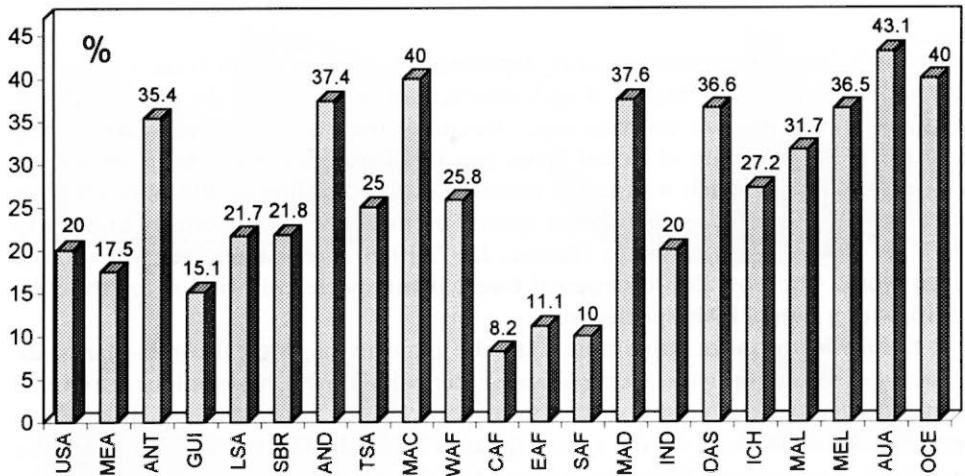


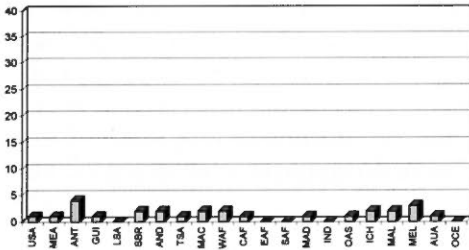
Fig. 6. The rate of epiphyllous endemism within different floristic regions of the world.

"weedy" species following human impact affecting tropical rainforest areas in Papua New Guinea. Invasion of alien species even in the understories of the rainforest can be serious. The author has observed the shrub or small tree size *Psidium cattleianum* invading the upland climax rainforest in Mauritius island, areas that originally were very rich in species, including epiphylls. Epiphyllous diversity seriously decreased with the appearance of *Psidium*, which oppressed all native shrubs, seedlings and herbaceous undergrowth. Although it is evergreen and the smooth surface seems to be suitable for epiphyll colonization, the uniformization of substrate (compared to the various hosts of intact forest) and probably the change of microclimate could cause a loss of diversity.

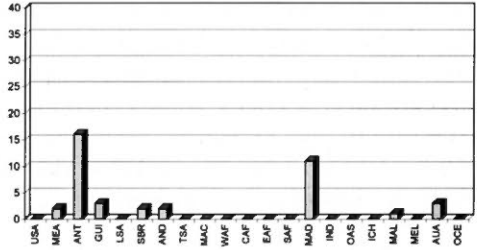
Other types of human interference, such as undercropping of rainforest by banana and cardamom, as seen in many places of the Usambara Mountains and in the Comoro Islands, also influences the epiphyllous growth by changing the microclimate and by opening the way for weedy species in the undergrowth, which are usually not suitable hosts for epiphylls. Even if the canopy is not opened, a serious impoverishment of epiphyllous vegetation can be observed.

In certain areas of the tropics, air pollution of an industrial origin prevents epiphyllous growth. Air pollution in the past few decades is no longer restricted to the industrialized northern temperate belt. A good example of a well documented case of tropical air pollution inhibiting epiphytic bryophyte growth is that of Ciudad Mexico reported by Durán *et al.* (1992). The only reference to the epiphylls in this connection can be cited from Reyes (1981), as follows: "Las hepáticas epifilas de la subfamilia *Cololejeuneoideae* así como otros grupos epifilos, representan un elemento importante como indicadores de la contaminación ambiental. Se ha observado que en las áreas industrializadas de Cuba, que coinciden además con

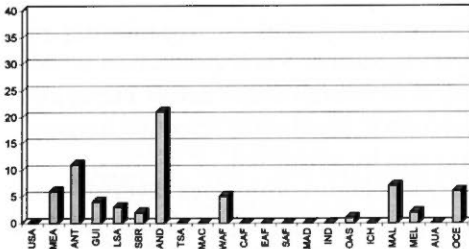
1. APHANOLEJEUNEA



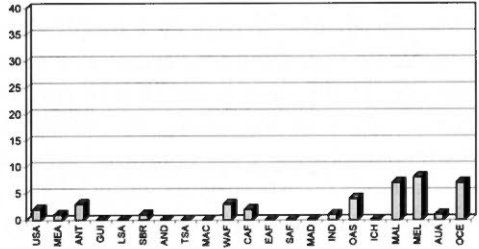
5. DIPLASIOLEJEUNEA



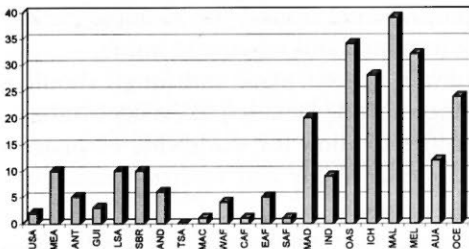
2. CERATOLEJEUNEA



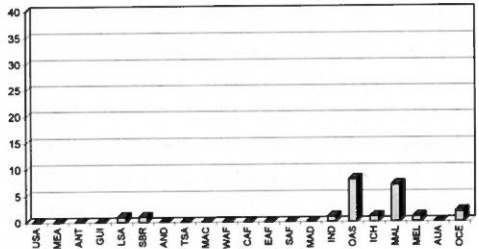
6. DREPANOLEJEUNEA



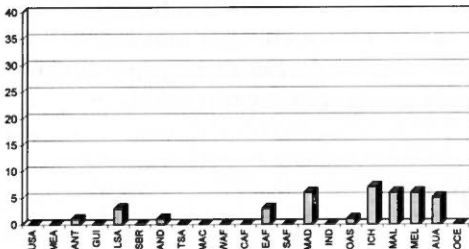
3. COLOLEJEUNEA



7. LEPTOLEJEUNEA



4. COLURA



8. MICROLEJEUNEA

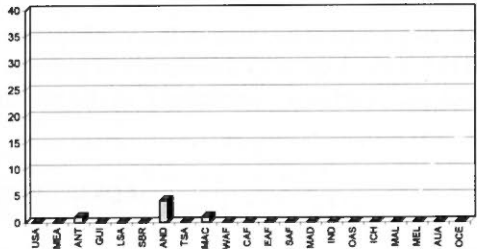


Fig. 7. The number of endemic epiphyllous species within different floristic regions of the world.

los elementos fitogeográficos y ecológicos requeridos por estos epifilos, como Moa, Nicaro, Santiago de Cuba; hay una ausencia total de hepáticas epifilas. Pongamos como ejemplo Monte Breña en Moa, lugar históricamente rico en colectas, con una vegetación de bosque siempreverde estacional; en esta zona llega de manera directa el aire contaminado de la planta procesadora de nickel de Moa." The author has personally seen this place and can document that within a distance of 10 km from the nickel works, there were no epiphylls at all in places otherwise suitable for their growth.

Proposed conservation measures

Most epiphyllous hepatics are too small to identify in the field and are fully dependant on the environment created by rainforest vegetation. Their protection is only possible by the total protection of certain well selected rainforest areas. Here, as a consequence of the above, no human interference (including selective logging, undercropping or even organized silviculture) can be permitted.

In each floristic region, especially in areas with high epiphyllous diveristy or a high rate of endemism, strictly protected forest reserves should be selected for this purpose. This measure should conform to the 'minimum programme' of conservation in tropical rainforest areas, according to Whitmore and Sayer (1992). This should be done within the existing network of national parks and protected areas, but in their untouched core, as further destruction of land around the national parks without a buffering zone can negatively affect the epiphyllous vegetation inside.

The folicolous flora of these plots (bryophytes, lichens, algae and fungi) should be catalogued and their synusia carefully monitored. Detailed diversity studies should be made on the epiphyllous communities to allow for worldwide comparison. Parallel the growth rate, life strategies, dispersal ability and environmental requirements of epiphylls should be investigated in detail.

The Lejeuneaceae have reached their evolutionary peak at present, with the highest diversity in tropical rainforest areas adapted to the special micro-environment of the phyllosphaere. There is no other ecological-taxonomic group within the Hepaticae comparable to the epiphyllous Lejeuneaceae, amounting half of all known Hepaticae, where the evolution takes place with such vigor and on such a large scale. Our responsibility is to preserve them, as their decline or impoverishment can mean serious interference in the evolutionary process of the plant world.

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LITERATURE CITED

- BISCHLER, H. 1964. Le genre *Drepanolejeunea* Steph. en Amérique Centrale et Méridionale. *Rev. Bryol. Lichénol.* 33: 15-179.
- BISCHLER, H. 1968. Notes sur l'anatomie des amphigastres et sur le développement du parapamhigastre et des rhizoïdes chez *Drepano*-, *Rhaphido*- et *Leptolejeunea*. *Rev. Bryol. Lichénol.* 36: 45-55.
- BUSSE, W. 1905. Über das Auftreten epiphyllischer Kryptogamen im Regenwaldgebiet von Kamerun. *Ber. dt. bot. Ges.* 23: 164-172.
- CHEN, P-C. AND P-C WU. 1964. Study of epiphyllous liverworts in China (I). *Acta Phytotax. Sinica* 9: 213-276.
- EVANS, A.W. 1902-12. Hepaticae of Puerto Rico I-XI. *Bull. Torrey Bot. Club* 29: 496-510; 30: 19-41, 544-563; 31: 183-226; 32: 273-290, 33: 1-25; 34: 1-34, 533-568; 35: 155-179; 38: 251-286; 39: 209-225.
- GOEBEL, K. VON. 1888. Morphologische und biologische Studien, 1. Ueber epiphytische Farne und Muscineen. *Ann. Jard. Bot. Buitenzorg* 7: 1-73.
- GOEBEL, K. VON. 1889. *Pflanzenbiologische Schilderungen, Epiphyten, 1 (III)*. Elwert'sche Verlagbuchhandlung, Marburg, pp. 147-236.
- GRADSTEIN, S.R. 1992a. Threatened bryophytes of the neotropical rain forest: a status report. *Trop. Bryol.* 6: 83-93.
- GRADSTEIN, S.R. 1992b. The vanishing tropical rain forest as an environment for bryophytes and lichens. In: J.W. Bates and A. Farmer (eds.), *Bryophytes and lichens in a changing environment*. Oxford Science Publ., pp. 232-256.
- GRADSTEIN, S.R. 1994. Lejeuneaceae: Ptychantheae, Brachylejeuneae. *Fl. Neotrop.* 62: 1-216.
- GRADSTEIN, S.R. AND T. PÓCS. 1989. Bryophytes. In: H. Lieth, and M.J.A. Werger (eds.), *Tropical rain forest ecosystems. Biogeographical and ecological studies*. Elsevier Sci. Publ., Amsterdam, pp. 311-325.
- GRADSTEIN, S.R., G.B.A. VAN REENEN AND D. GRIFFIN. 1989. Species richness and origin of the bryophyte flora of the Colombian Andes. *Acta Bot. Neerl.* 38: 439-448.
- GROLLE, R. 1984. Zur Kenntnis der Lejeuneoideae in Cuba (1). *Cyclolejeunea. Wiss. Ztschr. Friedrich-Schiller-Univ. Jena, Naturwiss. R.* 33: 759-764.
- HORIKAWA, Y. 1932. Die epiphyllen Lebermoose von Japan. *Bot. Mag. Tokyo* 46: 176-187.
- HYVÖNEN, J., T. KOPONEN AND D.H. NORRIS. 1987. Human influence on the mossflora of tropical rainforest in Papua New Guinea. In: T. Pócs, T. Simon, Z. Tuba and J. Podani (eds.), Proceedings of the IAB Conference of Bryoecology, Budapest-Vácrátót, Hungary, 5-10 August, 1985. *Symposia Biologica Hungarica* 35: 621-629.
- LUO, J.-S. 1990. A synopsis of Chinese epiphyllous liverworts. *Trop. Bryol.* 2: 161-166.
- MASSART, J. 1898. Les végétaux epiphyllés. *Ann. Jard. Buitenzorg*, suppl.2: 103-108.
- MILLER, H.A. AND H.O. WHITTIER. 1990. Bryophyte floras of tropical Pacific islands. *Trop. Bryol.* 2: 167-175.
- OLARINMOYE, S.O. 1975. Culture studies on *Radula flaccida* Lindenbergh & Gottsche. *J. Bryol.* 8: 357-363.

- PIIPPO, S. 1994. On the biogeography of Western Melanesian Lejeuneaceae, with comments on their epiphyllous occurrence. *Trop. Bryol.* 9: 43-57.
- PÓCS, T. 1978. Epiphyllous communities and their distribution in East Africa. In: C. Suire, (ed.), *Congrès International de Bryologie*, Bordeaux, 21-23 Novembre 1977, *Comptes Rendus. Bryophyt. Bibl.* 13: 681-714.
- PÓCS, T. 1982. An epiphyllous liverwort community from the Caucasus Mountains. *Bryol. Beitr.* 1: 13-22.
- PÓCS, T. 1989. A preliminary study of the undergrowth of primary and secondary submontane rainforests in the east Usambara Mountains, with notes on epiphytes. In: A.C. Hamilton and R. Bensted-Smith (eds), *Forest conservation in the east Usambara Mountains, Tanzania*, IUCN, Gland, pp. 301-306.
- PÓCS, T. 1996. New or little known epiphyllous liverworts, VI. *Papillolejeunea* gen. nov. from Papua New Guinea. *Acta Bot. Hung.* 40 (in press).
- PÓCS, T. AND B. TÓTHMÉRÉSZ. 1996. Follicolous diversity in tropical rainforests. In: E. Farkas and T. Pócs (eds.), *Proceedings of the IAB & IAL Symposium on Follicolous Cryptogams*. 29 August - 2 September 1995. Eger, Hungary.
- RAVEN, P.H. 1987. The scope of the plant conservation problem world-wide. In: D. Bramwell, O. Hamann, V. Heywood and H. Synge (eds.), *Botanic gardens and the world conservation strategy*. Academic Press, London, pp. 19-29.
- RAVEN, P.H. 1988. Our diminishing tropical forests. In: E.O. Wilson and F.M. Peter (eds.), *Biodiversity*. National Academy Press. Washington, DC., pp. 119-122
- REID, W.V. 1992. How many species will there be? In: T.C. Whitmore and J.A. Sayer (eds.), *Tropical deforestation and species extinction*. Chapman and Hall - IUCN, London, pp. 55-73.
- REYES, D.M. 1981. Estudio taxonómico y fitogeográfico de la subfamilia más importante de las hepáticas epifilas (*Lejeuneaceae: Cololejeuneoideae*) de Cuba. Thesis manuscript, 112+IX pp.
- RICHARDS, P.W. 1983. The three-dimensional structure of tropical rain forest. In: S.L., Sutton, T.C. Whitmore and A.C. Chadwick (eds.), *Tropical rain forest: Ecology and management*. Blackwell, Oxford, pp. 3-24.
- RICHARDS, P.W. 1984. The ecology of tropical forest bryophytes. In: R.M. Schuster (ed.), *New Manual of Bryology*, Vol.2. Hattori Botanical Laboratory, Nichinan. pp. 1233-1270.
- RUINEN, J. 1961. The phyllosphere. I. An ecological neglected milieu. *Plant and Soil* 15: 81-109.
- SCHUSTER, R.M. 1959. Epiphyllous Hepaticae in the Southern Appalachians. *Bryologist* 62: 52-55.
- SCHUSTER, R.M. 1980. *The Hepaticae and Anthocerotae of North America*. Vol. 4. Columbia University Press, New York.
- SCHUSTER, R.M. 1990. Origins of Neotropical leafy Hepaticae. *Trop. Bryol.* 2: 239-264.
- SJÖGREN, E. 1975. Epiphyllous bryophytes from Madeira. *Bot. Tid.* 69: 217-288.
- SJÖGREN, E. 1978. Bryophyte vegetation in the Azores Islands. *Mem. Soc. Broteriana* 26: 6-283.
- SPRUCE, R. 1884-1885. Hepaticae amazonicae et andinae. *Trans. Proc. Bot. Soc. Edinburgh* 15: 1-590, pls.1-22.
- STEPHANI, F. 1898-1924. *Species Hepaticarum I-VI*. Geneva.
- TAKHTAJAN, A. 1986. *Floristic regions of the world*. University of California Press, Berkeley.
- THIERS, B.M. 1990. An overview of the Lejeuneaceae in Australia. *Trop. Bryol.* 2: 273-283.

- VITT, D.H., M. OSTAFICHUK AND I.M. BRODO. 1973. Foliicolous bryophytes and lichens of *Thuja plicata* in western British Columbia. *Canadian J. Bot.* 51: 571-580.
- WHITMORE, T.C. AND J.A. SAYER. 1992. Deforestation and species extinction in tropical moist forests. In: T.C. Whitmore and J.A. Sayer (eds.), *Tropical deforestation and species extinction*. Chapman and Hall - IUCN, London, pp. 1-14.
- WINKLER, S. 1967. Die epiphyllen Moose der Nebelwälder von El Salvador C. A. *Rev. Bryol. Lichénol.* 35: 303-369.
- WINKLER, S. 1970. Zur Anatomie der Rhizoidenplatten neotropischer, holostiper Lejeuneaceen. *Rev. Bryol. Lichénol.* 37: 47-55.
- WU, P-C., D-K. LI AND C-H. GAO. 1987. Light and epiphyllous liverworts in the subtropical evergreen forests of South-East China. In: T.Pócs, T. Simon, Z. Tuba and J. Podani (eds.), Proceedings of the IAB Conference of Bryoecology, Budapest-Vácrátót, Hungary, 5-10 August, 1985. *Symposia Biologica Hungarica* 35: 27-32.