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DISJUNCT HEPATICAE IN TROPICAL AMERICA AND AFRICA

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An increasingly large number of macrodisjunct species is emerging from recent literature dealing with taxonomy and floristics of tropical bryophytes. This paper reviews present knowledge concerning Afro-American disjunctions in Hepaticae and seeks to interprete the data in the light of current phytogeographical theory. Numerous new floristic records and range extensions are given and some taxonomic novelties are proposed. For 35 Afro-American species known three main distribution types are recognized, each further subdivided: Tropical Afro-American (lowland, montane and the alpine element), Subtropical-Mediterranean (southern, wide element) and Temperate-Subantarctic (southern, wide element). Most species belong to Jungermanniales except for the subtropical ones which are thallose. A few Afro-American genera, including the "peri-Afroamerican" *Symbiezidium* and *Bryopteris*, and vicariant species-pairs are also discussed. Among tropical taxa, lowland patterns are normally continuous, while montane and alpine patterns are typically "quadricentric" resp. "bicentric". Deviating patterns may due to insufficient exploring or taxonomic knowledge, or relict nature. Several species are "weedy" and in the possession of excellent dispersal capacities; their occurrence in other palaeotropic regions is to be expected as well. Interpretation of dispersability is hampered, however, by the lack of experimental data on spore viability in liverworts (as contrary to mosses). It is postulated that macrodisjunct Afro-American species ranges in most cases should have arisen from successful transoceanic long-range dispersal whereas generic disjunction and species vicariance might be the result of ancient land connections, viz. evolution following the dissection of western Gondwanaland.

Introduction

"*The phenomenon of disjunct taxa has long fascinated phytogeographers and taxonomists, and few questions have been more discussed by various groups of botanists in recent decades*" (Löve 1967: 331).

In the 19th century there was a common belief, that the distribution of bryophyte species and of other spore plants was often world-wide (see e.g. Synopsis Hepaticarum, 1844–47). Later, the idea that bryophyte species are normally restricted to continents or smaller regions, became more widely accepted and led i.a. to an enormous increase in the number of described species (e.g. Stephani 1898—1924). In the past fifty years monographic studies have shown that this "geographical species concept" was ill-founded, and the true ranges of the species are now gradually becoming known. Macro-disjunct bryophyte species were discussed in recent papers by e.g. Grolle (1969), Schuster (1969, 1979), Schofield (1974), Schofield and Crum (1972), van Zanten and Pócs(1981) and Frahm (1982), but all of these, except the latter two are concerned with temperate rather than tropical patterns. The reason for the relative neglect of tropical disjuncts may be our still very incomplete knowledge of the taxonomy of tropical bryophytes and the deplorable state of the floristic inventory (see PRANCE 1977; GEISSLER and GREENE 1982). Nevertheless, it is evident that an increasingly large number of macro-disjunct species is emerging from recent literature dealing with tropical groups.

ARNELL (1958) was the first to give a tentative list of liverwort species common for both South America and South Africa. One of us (PÓCS 1976*a*) has recently inventoried the macro-disjunct bryophyte species for tropical Africa and Asia and could list no less than 108 "palaeotropic" species (35 liverworts, 73 mosses), known to occur in each of the two continents but not elsewhere. In addition, five other categories of macro-disjunctions among the species from Africa were recognized; Cosmopolitan species (65), Temperate species (111), Pantropical species (55), Subantarctic species (111) and Neotropical species (66). It is with the latter category — to be qualified more correctly as "Afro-American" — that we are dealing with in this paper. For practical reasons, we shall confine ourselves to the Afro-American liverworts.

Relationships among the tropical African and American floras were recently reviewed for flowering plants by THORNE (1973), who found many parallels and resemblances among the Angiosperm genera of the two regions. KORNAŚ (1981) gave a good account on the trans-oceanic disjunction between Africa and America and BORHIDI (1982) elucidated the special and ancient links between Caribbean and African floras.

For the bryophyte genera a comparison was made long ago by HERZOG (1926), who was able to demonstrate that bryofloristic similarities were greater among Africa and tropical America than among Africa and tropical Asia. While this would seem to indicate that a phytogeographic subdivision into "Neotropic" and "Palaeotropic" is unjustified, HERZOG (1926) nevertheless maintained this subdivision because among tropical regions tropical America has the largest number of endemics. It would be tempting to reconsider this matter using up-to-date phytogeographic information on the tropical bryofloras. In any case, we would like to point out that a higher affinity at the generic level between Africa and America could be explained by the more complete Gondwanalandic connection between the two continents.

Biogeographers distinguish at least two major types of disjunction among species (cf. FRYXELL 1967): 1. bicentric taxa, in which the disjunct populations are not differentiated, and 2. vicarious taxa, where the disjunct populations are differentiated at the specific ("species pairs") or infraspecific level ("geographic races", or more properly called, subspecies) (cf. VAN STEENIS 1957, TOUW 1982). Although we are dealing primarily with the bicentric species, vicarious taxa whose status has been verified by monographic work (including some genera with bicontinental distribution) are taken into consideration as well as their ranges and mode of dispersal may offer further insight in the characteristics and possible causes of the Afro-American disjunctions. Furthermore, we have made a working list of African and American species said to be closely related but of unverified status. This list serves as a basis in our further search for Afro-American distributions (Table 3).

There are different approaches to explain intercontinental disjunctions among bryophytes. Some of them (ANDERSON 1963, FULFORD 1963, CRUM 1972, SCHUSTER 1969, 1979, PÓCS 1976*a*, 1982*a*) underline the importance of geological events, especially of continental drift in the present distribution of bryophytes, which are (especially the Hepaticae) more conservative in their evolution, than phanerogams are. Others advocated the importance of long range dispersal: among southern temperate mosses VAN ZANTEN has shown correlations between the size of area of distribution and spore resistance and experimentally proved the survival ability of the spores of many species under conditions similar to those of high air currents (VAN ZANTEN 1976, 1978, 1979). Evidence opposing and supporting both views (and some others) is discussed at length by VAN ZANTEN and PÓCS (1981). Some of their final conclusions (l.c. 544–547) are:

A) *Land connections* prior to the continental drift are very important for the understanding of evolution and migration of bryophytes. In the more conservative groups (primitive Hepaticae and much less mosses) actual species levels might have been established already before the split of great land masses. In other liverwort groups and most mosses, however, these ancient land connections are considered as explanatory for present-day relationships at family-, genus- and at vicariant species pair level.

B) *Step by step dispersal* following geological or climatic changes on the continents (or on islands and isolated land masses not too far from each other) causes modifications in the distribution of bryophytes, possibly followed by isolation and speciation.

C) *Long-range dispersal* by aerial transport of diaspores between continents or other land masses can drastically modify the picture achieved by plate tectonics and step by step dispersal. The effectiveness of long-range dispersal depends on the following conditions:

1. Spores or propagules must be produced in large quantities.
2. Diaspores must be small enough for aerial transport. (In general not larger than 25 μm in diameter.)
3. The diaspores must have resistance to desiccation and freezing.
4. The arriving diaspores need suitable habitats, and
5. competing ability with the autochtonous vegetation.
6. The receiving area has to be large and varied enough to provide successful migration chances, finally
7. should possess unsaturated niches, not filled by autochtonous vegetation.

Concluding from the above, successful long-range dispersal becomes likely when the species is bisexual, possesses gemmae, occurs on young oceanic islands or is weedy in character, living on bare, often secondary surfaces (VAN ZANTEN and PÓCS 1981). As VAN ZANTEN established (in VAN ZANTEN and PÓCS 1981: 523) diaspores of tropical bryophytes have much less resistance to desiccation and freezing than temperate ones, therefore chances for successful transoceanic dispersal should be smaller in tropical species, especially in those belonging to the lowland element.

Results

Taxa, for which Afro-American distribution has been established, are listed in Tables 1 (bicontinental species and vicarious taxa), 2 (genera) and 3 (presumed Afro-American species pairs of unverified status).

Among the earliest species proved to be disjunct Afro-American are *Radula flaccida* and *R. stenocalyx* (CASTLE 1939), others, such as *Schiffneriolejeunea polycarpa* (GRADSTEIN 1974), *Kurzia capillaris* and *Lepidozia cupressina* (PÓCS 1983) and *Lophocolea martiana* (this paper) were long hinted at to be Afro-American in earlier literature before they finally proved to be so. For more than half of the species listed in Table 1 Afro-American distribution was demonstrated within the last ten years, e.g. through the work of Dr. E. W. JONES, Dr. R. GROLLE and others including the authors (GRADSTEIN 1974, 1980; BIZOT and PÓCS 1974; PÓCS 1977, 1983; VÁŇA 1980, 1982, VÁŇA et al. 1979). Many of them are the result of monographic comparisons between African and American taxa, but in some cases they resulted from new floristic discoveries, e.g. *Lejeunea autoica* (JONES 1979), *Gymnocoleopsis multiflora*, *Lophozia argentina* (VÁŇA 1982) or *Exormotheca pustulosa* (BISCHLER 1976). In other cases, e.g. *Herbertus subdentatus* (type from America), which was reported for Africa here for the first time, an African synonym has not yet been determined and remains to be detected among the various existing African binomina of the genus.

Not unexpectedly it turns out that for most of the Afro-American species type specimens originate from America, which should reflect the early date by which floristic explorations

Table 1

List of disjunct Afro-American liverwort species and vicarious taxa

Species or species pair	Altitudinal range*					Means of dispersal			Spore size if known, μm
	lowland	submontane	montane	subalpine	alpine	Gemmae or fragments	Spori		
							autoic	dioic	
Ia. Tropical lowland element									
1. *Acrolejeunea emergens*	+	+	—	—	—	+	+	—	45–60
2. *Aneura pseudopinguis*	+	+	+	—	—	—	—	+	13–16
3. *Cololejeunea cardiocarpa*	+	+	—	—	—	+	+	—	>40
4. *Lejeunea autoica*	+	(+)	—	—	—	—	+	—	>40
5. *Leucolejeunea unciloba*	+	+	—	—	—	—	+	—	23×40–50
6. *Lophocolea martiana*	+	—	—	—	—	—	+	—	?
7. *Mastigolejeunea auriculata*	+	—	—	—	—	—	+	—	>40
8. *Pycnolejeunea contigua*	+	+	—	—	—	—	+	—	>40
9. *Radula flaccida*	+	—	—	—	—	—	—	+	?
10. *Rectolejeunea brittoniae*	+	+	+	—	—	+	—	+	12–19× <
11. *Schiffneriolejeunea polycarpa*	+	+	—	—	—	—	+	—	?
12. *Arachniopsis dissotricha* and *diplopoda*	+	—	—	—	—	—	?	—	
Ib. Tropical montane element									
15. *Aphanolejeunea exigua*	—	+	+	—	—	+	+	—	?
16. *Arachniopsis diacantha*	+	+	+	+	—	?	+	—	?
17. *Kurzia capillaris*	—	+	+	—	—	—	—	+	12
18. *Radula boryana*	—	+	+	—	—	—	—	+	?
19. *Radula stenocalyx*	—	+	+	—	—	+	—	+	?
20. *Symphyogyna brasiliensis*	—	+	+	—	—	—	—	+	24–28
21. *Syzygiella concreta*	—	+	+	—	—	—	—	+	?
22. *Diplasiolejeunea pellucida* and *albifolia*	+	+	+	—	—	+	—	+	20× <
23. *Jungermannia amoena* and *borgenii*	—	+	+	—	—	—	—	+	18–22a 14–20b
24. *Leptoscyphus amphibolius* and *infuscatus*	—	—	+	+	—	—	—	+	13–15a
25. *Syzygiella manca* and *geminifolia*	—	—	+	+	—	—	—	+	24–32m

I ·ɔTropical alpine element									
27. *Andrewsianthus jamesonii*	—	—	+	+	+	+	—	+	15–18
28. *Gymnocoleopsis multiflora*	—	—	—	—	+	—	+	—	?
29. *Herbertus subdentatus*	—	—	+	+	+	—	—	+	?
30. *Isotachis aubertii*	—	—	+	+	+	—	—	+	?
31. *Marsupella africana*	—	—	—	—	+	?	—	+	10–12
32. *Stephaniella paraphyllina*	—	—	—	—	+	?	?	?	?
33. *Colura ornithocephala* and *kilimanjarica*	—	—	—	+	—	—	—	+	?
34. *Gongylanthus liebmannianus* and *scariosus*	—	—	+l.	—	+s.	—	—	?	25–29s.
35. *Lethocolea glossophylla* and *congesta*	—	—	+	+	+	+	+c.	+g.	?
II. Subtropical-Mediterranean element									
36. *Sphaerocarpos stipitatus*	+	—	—	—	—	—	—	+	tetrad 95–135
37. *Exormotheca pustulosa*	+	+	+	—	—	—	+	—	50–65
IIIa. Southern temperate element penetrating into tropical mountains									
38. *Clasmatocolea vermicularis*	+	+	+	—	—	—	—	+	16–20
39. *Heteroscyphus integrifolius*	?	?	+	—	—	—	+	—	?
40. *Hyalolepidozia bicuspidata*	+	+	—	—	—	?	—	+	12
41. *Lepicolea ochroleuca*	+	+	+	—	—	—	?	?	?
42. *Leptoscyphus expansus*	+	+	+	+	—	—	—	+	12
43. *Lophozia argentina*	—	?	?	+	—	—	—	+	?
44. *Schistochila alata*	+	+	+	—	—	—	—	+	17–23
45. *Tylimanthus limbatus*	+	+	+	—	—	—	—	+	?
IIIb. Wide southern temperate element penetrating up to Atlantic Europe									
46. *Adelanthus decipiens*	—	+	+	—	—	—	—	+	12–16
47. *Adelanthus lindenbergianus*	+	+	+	+	—	+	—	+	12–16
48. *Colura calyptrifolia*	+	+	+	—	—	+	+	—	20–30×40–65
49. *Lepidozia cupressina*	+	+	+	+	—	—	—	+	10–16
50. *Leptoscyphus cuneifolius*	—	+	+	+	—	+	—	+	?
51. *Lejeunea (Microlejeunea) ulicina* complex	+	+	+	—	—	—	—	+	?
52. *Telaranea nematodes*	+	+	+	+	+	—	—	+	14–16

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* Approximate ranges for altitudinal zones in the tropics are: lowland up to 800 m, submontane 800–1600 m, montane 1600–3000 m, subalpine 3000–3600 m, alpine above 3600 m. These values are valid in continental areas near the Equator, and much lower on oceanic islands and at higher latitudes.

started in South America and the inhospitality of the tropical African mainland to 18th and 19th century plant collectors. Where exist older African names, they are usually from the East African islands (e.g. *Acrolejeunea emergens, Isotachis aubertii*) or from the Cape (*Leptoscyphus expansus, Schistochila alata*).

Some of the Afro-American species discussed here may eventually turn out to be more widely distributed, especially where taxonomic studies are not yet world-wide. This is illustrated by the fact that among the bicentric Afro-Asiatic liverwort species listed recently by one of us (Pócs 1976), three have in the meantime proved to exist in tropical America as well and are thus in fact pantropical: *Anastrophyllum auritum* (Váňa 1982), *Iwatsukia jishibae* (Váňa 1980) and *Radula javanica* (Yamada in litt.).

Although we would define Afro-American species in a strict sense as those restricted in their distribution to the African mainland and its surrounding islands as well as tropical and antipodal America, we would include here in this category as well those species with optimal occurrence in these regions but with occasional extensions into adjacent regions, e.g. Europe (Mediterranean and atlantic, Western Europe) or along the atlantic coast of North America and Ceylon. The latter island was considered to act as easternmost limit for the range of several Afro-American Lejeuneaceae by Gradstein and Inoue (1980).

Grolle (1969) discussed some examples of Afro-American distribution types among liverwort species and recognized two floristic elements:

a) Tropical element (*Arachniopsis diacantha*).

b) Subantarctic element (*Adelanthus lindenbergianus, A. decipiens* and *Stephaniella paraphyllina*). The latter species in our opinion does not belong here.

Frahm (1982) reviewed the distribution of five Afro-American species of *Campylopus* and recognized three elements:

1. Southern temperate (subtropical) element,
2. Tropical-montane element,
3. Afroalpine-andine element.

While his first element seems to correlate with Grolle's subantarctic element, and the other two with Grolle's tropical element, his comparing the distribution of *Adelanthus lindenbergianus* and *A. decipiens* with that of the Afroalpine-andine element suggests, that the two classifications were not based entirely on the same principles.

A comparison of the maps and altitudinal distributions of the Afro-American liverworts discussed in this paper reveals the following geographical patterns (see also Table 1):

I. TROPICAL AFRO-AMERICAN
  a) Tropical lowland element (lowland-submontane)
  b) Tropical montane element (submontane-montane)
  c) Tropical alpine element (montane-alpine)
II. SUBTROPICAL-MEDITERRANEAN AFRO-AMERICAN
  a) Southern subtropical element
  b) Widely distributed element
III. TEMPERATE-SUBANTARCTIC AFRO-AMERICAN
  a) Southern temperate element
  b) Widely distributed element

I. TROPICAL AFRO-AMERICAN ELEMENTS

From Table 1, where the bicontinental tropical species and vicariants are listed according to their vertical, altitudinal distribution, the three main tropical elements become apparent. Division into altitudinal zones is according to

TROLL (1961) and regional literature (e.g. HEDBERG 1951, PÓCS 1976*b*, CUATRECASAS 1954, CLEEF 1978). A few species of the above category could not be placed with certainty in one of the three elements. Their placement should remain tentative pending further study.

I.a. Tropical lowland element

1. Acrolejeunea emergens (Mitt.) Steph. (Lejeuneaceae) (Plate I/1)

Widespread in tropical Africa (lacking in S. Africa) from sea level up to 1500 m. In tropical America of more restricted occurrence and known only from few collections of mainland S. America and Central America (GRADSTEIN 1975). Recently the species was reported also from Ceylon, previously identified as *A. fertilis* (GRADSTEIN and INOUE 1980).

Acrolejeunea emergens is a rather xerotolerant species occurring as an epiphyte in mesic forests, deciduous savanna woodlands, often together with the Afro-American *Schiffneriolejeunea polycarpa* and *Mastigolejeunea auriculata* and with the pantropical *Frullania ericoides* (cf. also PÓCS 1982*b*).

It is usually monoicous and produces spores as well as gemmae (caducous leaves) in great amount. GRADSTEIN (1975) suggested a West Gondwanic origin for *Acrolejeunea* subgenus *Acrolejeunea* (which includes *A. emergens*) and early tertiary migration towards its present area of distribution (tropical America including subtropical Central Florida, tropical Africa, Indo-China and Japan). Since *A. emergens* possesses copious means of dispersal, it seems unnecessary to postulate a Gondwanic origin for this *species* as an explanation of its present area of distribution.

2. Aneura pseudopinguis (Herz.) Pócs comb. nova (Aneuraceae) (Plate I/2)

Basionym: *Riccardia pseudopinguis* Herzog, Beih. Bot. Centralbl., Abt. B, 62; 560, Fig. 1a–b (1942).

Synonym: *Riccardia submarginata* S. Arnell, Bot. Not. 1953; 139.

Aneura pseudopinguis was not long ago described by HERZOG from Brazil. JONES in his account of African *Riccardia* (JONES 1956) does not mention other species of *Aneura*, as *A. pinguis*. ARNELL (1963: 86) was the first to recognize that some South African plants are identical with the American taxon. Later VANDEN BERGHEN (1972*b*) published it from tropical Africa. PÓCS (unpublished material) has recorded it both from East and West Africa (Tanzania; Ukaguru Mts. and from the Ivory Coast). HERZOG (l.c.) gave very good description and figures of reproductive characters to distinguish this species from the related *Aneura pinguis*, namely the spores of *A. pseudopinguis* are of much smaller size and the atheridial branches are long and many paired. Although ARNELL gives vegetative characters too (ARNELL 1963: 86), based on the size of thallus cells, these characters seem to be in contradiction with his own account on Scandinavian *A. pinguis* (ARNELL 1956: 30). Therefore we regarded to be confirmed only the records of plants possessing either male branches or spores.

A. pseudopinguis is dioicous and in African samples usually only one sex is found in each locality. Vegetative reproduction is not known. In Africa it lives in humid lowland and montane forests, on muddy earth banks or on rotting wood, between altitudes of sea level and 1900 m. The type locality in Brasil seems to be somehow secondary ("Nähe des Stausees, Kraftwerk am Brachino"). If it is not a recent introduction into tropical America, records of the species can easily be hidden under neotropical *R. pinguis* records, as already HERZOG (l.c.) remarked. The South American *Aneura latissima* Spruce and *A. laurentiana* Steph. should also be checked for possible synonymy.

3. **Cololejeunea cardiocarpa** (Nees et Mont.) Schust. (Lejeuneaceae) (Plate I/3)

A species common in coastal tropical America (West Indies, Galapagos Is., etc.) but almost lacking in the inner Amazon basin (cf. SPRUCE 1884–85). In contrast, most African records are from inland, from Kenya to Zimbabwe. In the Cape ARNELL (1963; 174–176) recorded it under the name of *Leptocolea cristata* and *L. cristata* var. *lanciloba*; the description accompanied by pictures clearly refers to *C. cardiocarpa*. Additional records from Madagascar and New Caledonia (hence pantropical distribution) are confirmed recently by TIXIER (1979: 748). *C. cardiocarpa* is usually epiphyllous, but lives often among rather dry conditions not fit for most of the epiphyllous species. It has a wide ecological tolerance, occurring from lowland to lower montane forests up to 1500 m (in Zaire, on Mt. Kahuzi as high as 2300 m) under humid to subxeric conditions. In Cuba it is often the only epiphyllous species in semidry riverine forests. On the Galapagos Islands it is one of the most common liverworts (GRADSTEIN and WEBER 1982). As this liverwort flora is of recent origin and presumably has arisen via transoceanic air dispersal, the present distribution of *C. cardiocarpa* might best be explained by long-range migration. Moreover, the species is monoicous and produces copious spores as well as gemmae.

4. **Lejeunea autoica** Schust. (Lejeuneaceae) (Plate I/4)

A rare and remarkably disjunct species with localities in Florida (the type) and in tropical West Africa, where it was recently discovered by JONES (1979). According to Dr. JONES the West African populations are morphologically slightly different from the American ones, but "too closely allied . . . to justify separating them as a different species" (JONES 1979; 391).

Lejeunea autoica occurs in humid lowland or submontane forests (subtropical Florida at sea level, Ghana 730 m. Mt. Cameroun 1160 m) as a sciophilous epiphyte, rarely over rock, and tends to grow mixed among other (larger) bryophytes. Its tiny habit and likeness to other Lejeuneae, as well as our poor knowledge of this notoriously difficult, yet very common tropical genus, suggest that the actual distribution patterns of *L. autoica* is little more than a testimony of our incomplete understanding of the genus *Lejeunea*.

Lejeunea autoica is usually copiously fertile, yet mature sporophytes have not yet been recorded. Vegetative reproduction is unknown in this species.

5. **Leucolejeunea unciloba** (Lindenb.) Evans (Lejeuneaceae) (Plate I/5)

Widespread in tropical America, but known only from scattered localities — in the West Indies almost lacking — except in the coastal plain of southeast U.S.A. from where are many records (SCHUSTER 1980). In Africa *L. unciloba* is rare and thus far only known from South Africa (Cape, Natal) and from Tanzania, where it was recently collected by Dr. JONES (JONES 1973) in submontane rain forest and on roadside trees. In tropical America it is apparently a mesophytic to almost xerophytic species, occurring on smooth bark of trees and shrub as well as on rock. In Brazil it is found in Amazonian forests (leg. SPRUCE) as well as dry cerradao shrub. In Colombia the species was found not to be uncommon as a crown epiphyte in montane forests up to 2500 m (GRADSTEIN unpubl.) although there was only one previous record for the country. In Cuba it lives in semidry rock forests together with the monotypic *Microcycas calocoma* (GROLLE 1975). Apparently the species has been overlooked in the past as may be true for other crown epiphytes (e.g. *Pycnolejeunea contigua*). *L. unciloba* is autoicous and usually fertile, yet mature sporophytes are rarely recorded. Vegetative reproduction is unknown in the genus.

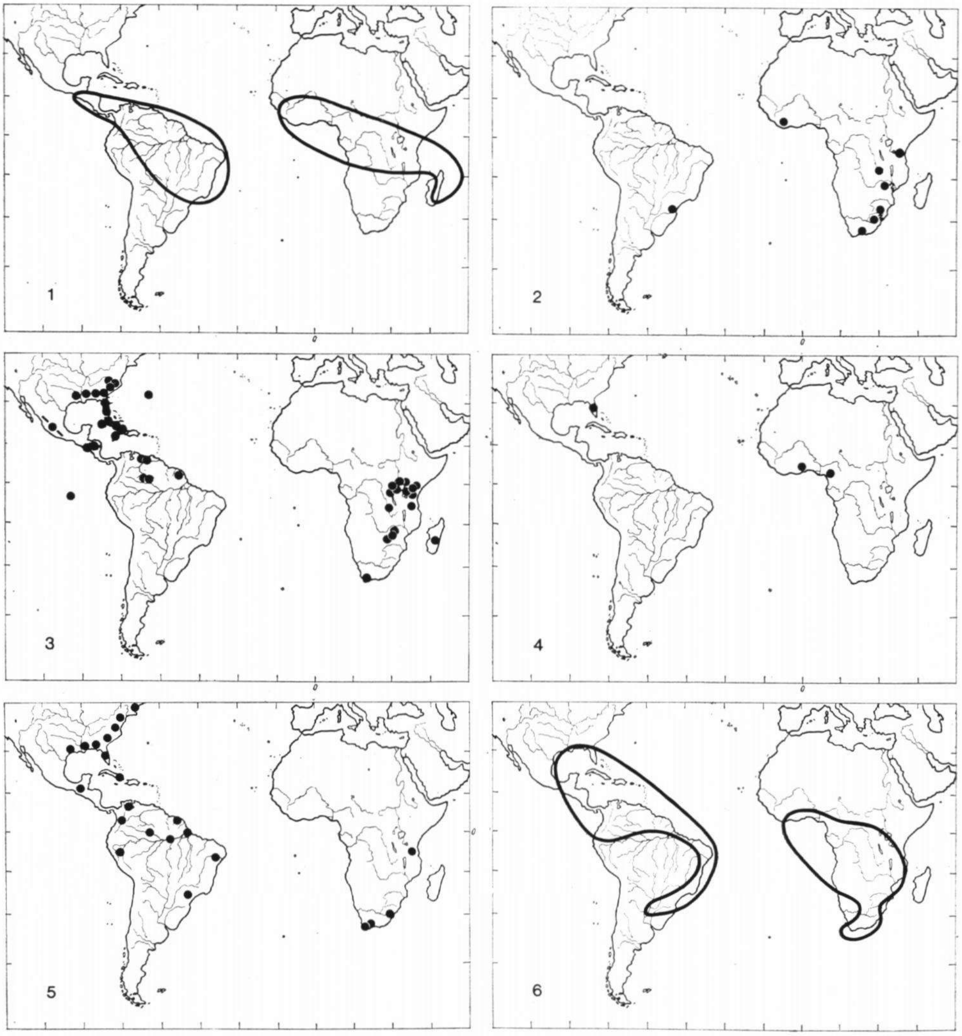

Plate I

Tropical lowland species. 1. *Acrolejeunea emergens* (Mitt.) Steph. (+Sri Lanka). 2. *Aneura pseudopinguis* (Herz.) Pócs. 3. *Cololejeunea cardiocarpa* (Nees et Mont.) Schust. (+N. Caledonia). 4. *Lejeunea autoica* Schust. 5. *Leucolejeunea unciloba* (Lindenb.) Evans. 6. *Lophocolea martiana* Nees.

6. **Lophocolea martiana** Nees in G., L. et N., Syn. Hep. 152 (1845) (Geocalycaceae) (Plate I/6)

Syn. nov.: *Lophocolea congoana* Steph., Sp. Hep. 3: 170 (1907)
L. dusenii Steph., Sp. Hep. 3: 178 p.p. (1907)
L. newtonii Steph., Sp. Hep. 3: 170 (1907)

L. martiana is a very common species of rather mesic lowland forests of the West Indies, southeastern Brazil and also West Africa, where the species was known for a long time as *L. newtonii* or *L. congoana*. Their close relationships with *L. martiana* were noted by several authors (EVANS 1905, JONES 1953, SCHUSTER 1980) and JONES (l.c.) hesitated to recognize the African and American species as different but decided to maintain them because "the South American plants themselves appear to be in need of further study" (p. 191). A careful comparison by one of us (VÁŇA, msc.) in the course of a study of Cuban Lophocoleaceae revealed the published differences as non-existing.

L. martiana appears to be particularly common in Atlantic coastal regions but is more rare in lowland areas, at least in South America. In East and South Africa it also becomes more sporadic, occurring rarely and isolated in lowland forests. The species grows on rotten wood, or rarely on earth, in lowland and in submontane forests up to 1500 m altitude, rarely higher. It is monoicous and often fertile; gemmae are unknown.

7. **Mastigolejeunea auriculata** (Wils.) Schiffn. (Lejeuneaceae)

One of the commonest species of Lejeuneaceae in lowland tropical America and Africa with a rather wide ecological tolerance yet probably not very xerotolerant as it is absent from the Galapagos Islands (GRADSTEIN and WEBER 1982). In Africa the species was known as *M. carinata* (Mitt.) Steph. which was synonymized with *M. auriculata* by GRADSTEIN and INOUE (1980). The species also occurs on Ceylon and possibly elsewhere in Asia where a closely related and rather polymorphic species (*M. humilis*) occurs. Further revisionary work is needed to establish the actual distribution pattern of this species. *M. auriculata* is polyoicous (autoicous or dioicous) and may disperse by spores; gemmae are unknown in this genus.

8. **Pycnolejeunea contigua** (Nees) Grolle (Lejeuneaceae) (Plate II/7)

A tropical American species — with a confusing nomenclatural history (GROLLE 1979) — which was recently discovered in tropical Africa by JONES (1979). According to Dr. JONES the species grows in West Africa in humid lowland rain forests as a crown epiphyte of large canopy trees, and has therefore likely been overlooked in the past (JONES 1979). In Tanzania it grows on bark at 1650 m, in an open ericaceous heath, above waterfalls. It apparently lacks in the drier, deciduous forests. About its neotropical habitat little is known. It should be a lowland forest species there, not uncommon in the Amazon basin (fide SPRUCE). Dr. VITAL has found it on tree bases in São Paulo State. The species is autoicous, but mature sporophytes have not yet been recorded. Vegetative reproduction is yet unknown.

9. **Radula flaccida** Lindenb. et Gott. (Radulaceae) (Plate II/8)

Widespread in tropical Africa as well as in tropical America where it occurs from Florida (probably extinct there fide SCHUSTER 1980) southwards to Amazonia and also in the rainforest near Buenos Aires (leg. TONDUZ 1892, now probably extinct as well). The species is a common epiphyllous, occasionally corticolous element in humid tropical lowland rainforests, occurring at altitudes from sea level to 1000 m. It is dioicous but produces perianths (and spores?) frequently. In addition it has copious production of multicellular, leaf-born gemmae, which, considering their size should be effective means for short distance dispersal.

With *R. stenocalyx* (below) *R. flaccida* belongs to a pantropical group of about ten, chiefly epiphyllous species: *Radula* sect. *Epiphyllae* Castle ex Grolle (CASTLE 1968, YAMADA 1979). Except for the Afro-American *R. flaccida* and *R. stenocalyx* the species are supposedly confined to single continents, with 5 species occurring in Asia (all of them widespread). SCHUSTER recently (1980) regrouped these species and left only *R. flaccida* and the East African *R. pseudoflaccida* in the sect. *Epiphyllae* Castle ex Grolle emend. Schust.

10. Rectolejeunea brittoniae Evans (Lejeuneaceae) (Plate II/9)

Since it was described from the Bahamas (Evans 1911), the species became known also from the greater Antilles and from Florida (Schuster 1980), where it seems to be quite widespread. Its African occurrence was hidden by the confusing synonymy clarified by Jones (1974), who gave a new name to the African plant: *Rectolejeunea arnellii* E. W. Jones recorded

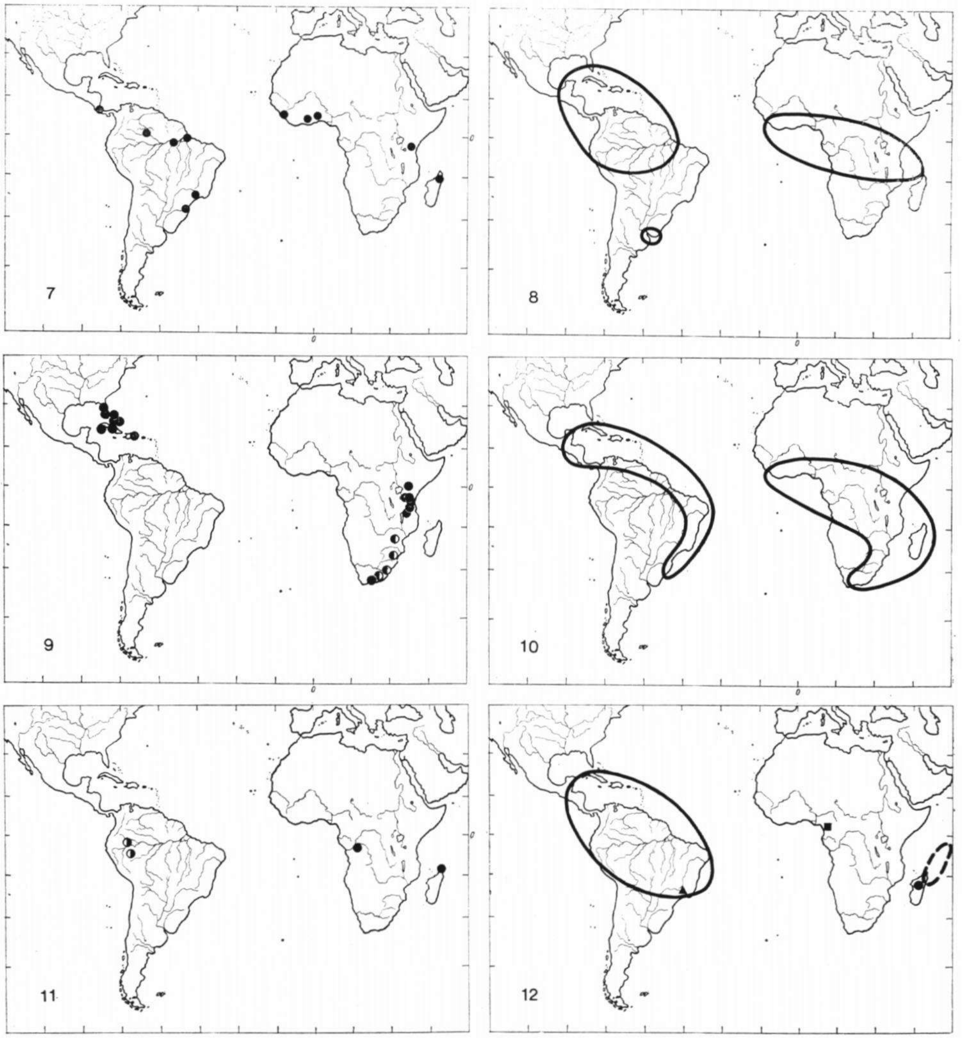

Plate II

Tropical lowland species. 7. *Pycnolejeunea contigua* (Nees) Grolle. 8. *Radula flaccida* (Lindenb.) Gott. 9. *Rectolejeunea brittoniae* Evans. (half dots: unconfirmed records). 10. *Schiffneriolejeunea polycarpa* (Nees) Gradst. (+Sri Lanka, S. India). 11. *Arachniopsis dissotricha* Spruce (half dots) and *A. diplopoda* Pócs (full dots). 12. *Haplolejeunea* Grolle and *Symbiezidium* Trev. Full circle: *H. sticta* Grolle; square: *H. cucullata* (Steph.) Grolle; triangle: *H. spec.* Continuous line: *S. transversale* (Sw.) Trev. and *S. barbiflorum* (L. et G.) Trev.; broken line: *S. madagascariense* Steph.

from Tanzania and from the Cape, Knysna, from where it was published under the name of *Rectolejeunea rhodesiae* (Sim) S. Arnell by ARNELL (1963). Other SE African records remained unconfirmed. PÓCS (in OCHYRA and PÓCS 1983) recorded the species also from Mt. Kenya. SCHUSTER considers *Rectolejeunea brittoniae* and *R. arnellii* synonymous, thus the species is bicentric in distribution. It occurs near the sea level in Florida and on the Bahamas, becomes submontane on the greater Antilles, is again a lowland species in subtropical South Africa, while definitely montane in East Africa, occurring between 1500 and 3300 m (Mt. Kenya). *Rectolejeunea brittoniae* is in most cases corticolous or even ramicolous, living on tiny twigs. Only one case (Mt. Kenya) it was found on rotten logs. It generally occurs in deep shade of closed tropical forests, but can occur in more open vegetation types as well, when humidity is high.

R. brittoniae is dioicous and often produces perianths; mature sporophytes were observed only in America. The spores are relatively small, 12–19 μm in diameter. Vegetative reproduction is known by caducous leaf lobes, which leave long sections of the stem often naked. They develop on almost unmodified shoots. The fallen (and even the unfallen) lobes often produce new plantlets from their marginal cells. Although the peculiar bicentric distribution pattern is still difficult to explain, the freely developing caducous lobes seem to enhance long-range aerial dispersal for this species.

11. **Schiffneriolejeunea polycarpa** (Nees) Gradst. (Lejeuneaceae) (Plate II/10)

This species is widespread in tropical and South Africa, but in tropical America it seems to be largely restricted to coastal regions along the Atlantic Ocean and the West Indies. It grows as an epiphyte in rather mesic to subxeric evergreen forests, in cerradao shrub, in deciduous woodlands, orchards and on roadside trees, at altitudes from sea level up to 1500 m. Its distribution area was recently expanded with reports from Ceylon (GRADSTEIN and INOUE 1980) and Southern India (UDAR and AWASHTI 1982), but the Indian and part of the Ceylonese populations are from higher altitudes (1500–2200 m) and are morphologically slightly different (tubulose female bracteole, cf. UDAR and AWASHTI 1982, Fig. 1: 1, 20), indicating that a separate subspecies might be at hand. The specimens from lower altitudes on Ceylon, however, are fully identical to the Afro-American populations and represent the easternmost extension of the area of the species known thus far. Similar distribution patterns are known for *Acrolejeunea emergens* and *Mastigolejeunea auriculata.*

A closely related vicariant species, *S. pulopenangensis* (Gott.) Gradst., occurs in Indomalesia.

S. polycarpa is autoicous and produces sporophytes freely. Vegetative reproduction is unknown. Its present distribution area resembles that of the cactus *Rhipsalis baccifera* (THORNE 1973, Fig. 1).

12. **Arachniopsis dissotricha** Spruce and **Arachniopsis diplopoda** Pócs (Lepidoziaceae) (Plate II/11)

The two *Arachniopsis* species form an interesting vicariant pair of related species within an isolated group of the genus. *A. dissotricha* is known since long from the upper Amazonian basin, both Brazil and Peru (SPRUCE 1882, 1885: 357, FULFORD 1968: 364). *A. diplopoda* became known by a collection made by G. CREMERS in northern Madagascar, from the herbarium of M. ONRAEDT, described, as a new species, by one of us (PÓCS 1984). An additional locality of the same species has been discovered from herbarium material (BR) collected by

Table 2

Liverwort genera largely restricted to America and Africa

Alt. range	Genus	Family	Total species	American species	African species	Species elsewhere
Trop. lowl.	*Arachniopsis*	Lepidoziac.	4	3	2	—
Trop. mont.	*Bryopteris*	Lejeuneac.	7	6	1	—
Trop. lowl.	*Haplolejeunea*	Lejeuneac.	2–3	1	2	—
Southern + tr. mont.	*Leptoscyphus*	Geocalycac.	24	19	6	2 Europe Azores
Trop. mont.	*Marchesinia*	Lejeuneac.	ca. 8	4 ?	3 ?	1 Europe
Trop. lowl.	*Odontolejeunea*	Lejeuneac.	ca. 5	4 ?	1–2	—
Trop. alp.	*Stephaniella*	Gymnomitriac.	5–6	5–6	1	—
Trop. lowl.	*Symbiezidium*	Lejeuneac.	3	2	1	—

C. J. MARTIAL-VOETS in Zaire (Mayumbé). It was found at both localities near sea level' intermixed in the wefts of *Sprucella succida* covering the soil surface or litter on the ground of dense or semishaded equatorial forest. We do not have information about the ecology of the American species collected at both localities only by SPRUCE, but his statement suggests a similar habitat: "Ad fluvium Uaupés, in rivuli ripis umbrosis arborum radices investiens" (SPRUCE 1885: 357).

Arachniopsis dissotricha is dioicous, while *A. diplopoda* is known only in sterile state. Vegetative means of reproduction are unknown. These facts, together with the peculiar, very isolated and disjunct distribution of two related species seem to confirm their common Gondwanalandic origin and speciation since the Gondwana dissection. Their present distribution should thus be considered as of relict nature. The possibility of long-range air dispersal as an explanation for their distribution is almost to be excluded.

13. Haplolejeunea Grolle (Lejeuneaceae subfam. Tuyamaelloideae) (Plate II/12*a*)

The Afro-American genus *Haplolejeunea* was recently described by GROLLE (1975, 1979) and is comprised of two or three species: *H. sticta* Grolle from submontane Madagascar, *H. cucullata* (Steph.) Grolle from Cameroun and an unnamed species from São Paolo State, Brazil (close to *H. cucullata* and possibly identical). As each species is based on a single collection only, very little can be said about their distribution although they are apparently rare as they never turned up among the numerous African collections of Lejeuneaceae made by Dr. JONES and others (GROLLE 1979).

The species are autoicous but mature sporophytes have not yet been observed. Gemmae are known in other members of Tuyamaelloideae but not in *Haplolejeunea.*

Haplolejeunea is the only African and tropical American representative of this mainly tropical Asiatic (*Tuyamaella*) and eurysubantarctic (*Siphonolejeunea*, *Austrolejeunea*, *Nephelolejeunea*) subfamily. As *Haplolejeunea* was suggested to be the most primitive member of the subfamily its current distribution may be considered of relict nature similarly to the above *Arachniopsis* species.

14. Symbiezidium Trev. (Lejeuneaceae subfam. Ptychanthoideae) (Plate II/12*b*)

Known from tropical America by two common, widespread species, each with many synonyms: *S. barbiflorum* and *S. transversale* (VAN BEEK and GRADSTEIN, msc.). The old (18th century!) records of *S. transversale* from Hawaii [as *S. cryptocarpum* (Mitt.) Trev.] and from Tasmania [as *S. bacciferum* (Tayl.) Trev.] are unconfirmed, doubtful and probably based on erroneous labels (VAN BEEK and GRADSTEIN, msc.). A third species, *S. madagascariense* Steph., is known from Africa where it occurs on Madagascar (type) and the Seychelles (GROLLE 1978) but lacks on the mainland. The African and American species are very different, probably representing subgeneric groups, and thus indicating a long-time separation. The peculiar disjunction in *Symbiezidium* might better be explained by ancient continental movements following an early evolution in the eastern portion of Gondwanaland, rather than by long-distance dispersal, in which case its absence from mainland Africa would be very difficult to explain.

Symbiezidium does not stay alone with its peculiar distribution pattern. There are three moss genera following the same pattern: *Phyllogonium* and *Potamium* (RENAULD et CARDOT 1915: 8, HERZOG 1926: 215, JOVET-AST 1948: 46), finally *Adelothecium* (CROSBY 1976: 712). There are also unconfirmed records on the occurrence of the neotropical genus *Drepanophyllum* from Réunion Island (uncertain according to RENAULD 1897: 121).

The phenomenon, namely, that tropical American plants occur in Lemuria being absent in continental Africa, is well known among phanerogamic genera. Similar disjunctions have also been reported by MOORE (1973) for ceroxyloid palms and by BORHIDI (1982: 237–239) for *Echinochlaena* (Poaceae, 6 American and 1 Lemurian species, none in continental Africa), *Oliganthes* (Asteraceae, 12 American and 9 Lemurian species, none in continental Africa), *Carpodiptera* (Tiliaceae, 5 + 1 species of the same pattern), *Oplonia* (Acanthaceae, 13 + 5 species), *Phenax* (Urticaceae, 25 + 3 species), *Rheedia* (Clusiaceae, 37 + 13 species), *Ravenala* (Musaceae, 1 American + 1 Madagascan species which occurs on Zanzibar Island too, but not in mainland Africa). These genera, called "peri-Afroamerican" element, are interpreted by STEARN (1971), as developed before the dissection of the Afro-American supercontinent and, at the time of the dissection, lacking in the interior of this enormous land mass, where drastic continental climate changes made them extinct. Therefore the formal central part of the supercontinent bears an impoverished flora and some coastal areas of the two continents are richer in these Gondwanalandic elements. BORHIDI (l.c.) provides much evidence in favour of STEARN's theory based on his analysis on the Cuban phanerogamic flora. The same phenomenon is known in the distribution of some animals, e.g. reptiles.

In tropical America the species of *Symbiezidium* occur as epiphytes in moist tropical lowland and submontane forests, but they are lacking in more mesic areas. Thus, the genus is common on Cocos Island, where there is plenty of moist primary forest, but lacks entirely on the more mesic Galapagos islands (GRADSTEIN and WEBER 1982). The plants are autoicous and dispersal should be by spores.

I.b. Tropical montane element

15. Aphanolejeunea exigua Evans (Lejeuneaceae) (Plate III/13)

Many localities are known of this tiny epiphyllous species from the montane forests of the Caribbean region, with some extention southwards to Brazil and northwards to Cuba and Mexico. It became known from East Africa only recently (PÓCS 1978: 693–694, without precise localities), where lives in the montane rain forests of the Ulugurus and Mt. Kilimanjaro. The altitudinal range of the species in the more equatorial montane areas lies between 1000–3000 m, but descends much lower in islands, like in Cuba (400–1000 m, REYES ined.).

It is probably much more widespread in tropical Africa, first of all in the East African mountains, but due to its microscopic size escaped the attention of the non-hepaticologist collectors.

The species is monoicous and produces spori and gemmae as well.

16. **Arachniopsis diacantha** (Mont.) Howe (Lepidoziaceae) (Plate III/14)

Arachniopsis is a typical Afro-American genus and *Arachniopsis diacantha* is its most widely distributed representative, which covers the whole range of the genus, being distributed in East Africa from Rwanda to Cape in the West from Sierra Leone to Gabon, on Madagascar and the Mascarenes. In America is known from Cuba through the Venezuelan, Colombian and Peruvian Andes to the Amazonian basin, where it was known under the name of *A. coactilis.* Based on examination of the types and a wide selection of specimens, PÓCS (1984) proved that *A. coactilis* does not differ specifically from *A. diacantha* and merits, at most varietal rank in which case its name should be *A. diacantha* var. *filifolia* (Spr.) Pócs. As there are many transitional forms within the whole range of distribution, the varieties are sympatric (see also GROLLE 1969: 578, Fig. 11/3).

The species occurs both in Africa and in America from almost sea level up to high altitudes, but it is commonest in wet submontane rain forests. In Venezuela *A. diacantha* goes up to 2000 m altitude, while in East Africa, on Mt. Kilimanjaro, it ascends as high as 2850 m in giant heather (*Erica arborea*) forest, almost reaching the forest line. It lives always on the shady, wet ground of rain forests, either on soil surface or more often on dead wood and litter, occasionally also on living bark or leaves. It seems to be strongly acidophilous, living together with other Lepidoziaceae (*Kurzia*, *Lepidozia*, *Bazzania*, *Telaranea* and in Africa also with *Sprucella*) species. *A. diacantha* is polyoicous, usually freely produces perianths although sporophytes are rare. Regeneration from leaf segment tip cells is described by FULFORD (1968: 362) and the detached, rhizoid bearing cells might serve as tools in vegetative reproduction.

17. **Kurzia capillaris** (Sw.) Grolle (Lepidoziaceae) (Plate III/15)

The widespread Afro-American *Kurzia capillaris* and its relatives were recently investigated by PÓCS (1984). The African taxon was first treated as a variety of American *Lepidozia capillaris*, under the name of var. *sterilis* Gott., Lindenb. et Nees. Later it was distinguished from the American species by STEPHANI, as *Lepidozia tabularis* Steph. [= *Microlepidozia tabularis* (Steph.) S. Arn., *Kurzia tabularis* (Steph.) Grolle]. Large amounts of material studied from both continents proved that none of the differences given by STEPHANI are stable and the American *Kurzia capillaris* and the African *K. tabularis* are therefore considered identical (PÓCS 1983).

Two other related taxa, *Lepidozia verrucosa* Steph. [= *Kurzia verrucosa* (Steph.) Grolle] and *Lepidozia stephanii* Ren. in Steph. [*Kurzia stephanii* (Ren.) Grolle] fall also within the range of variation of *Kurzia capillaris. K. stephanii* has leaf segments with their longest part consisting only one cell row and the segments in general are much smaller than those of the typical *K. capillaris.* In addition, it is restricted in its distribution to Madagascar, the Mascarenes and the old crystalline blocks of East Africa (Uluguru and Mulanje Mts.). Therefore its separation at subspecies level was proposed, as *K. capillaris* ssp. *stephanii* (Ren.) Pócs (l.c.).

Kurzia verrucosa differs from typical *K. capillaris* only in its stronger papillosity of the leaf cuticles. As the two taxa are sympatric in distribution, it merits only the rank of variety:

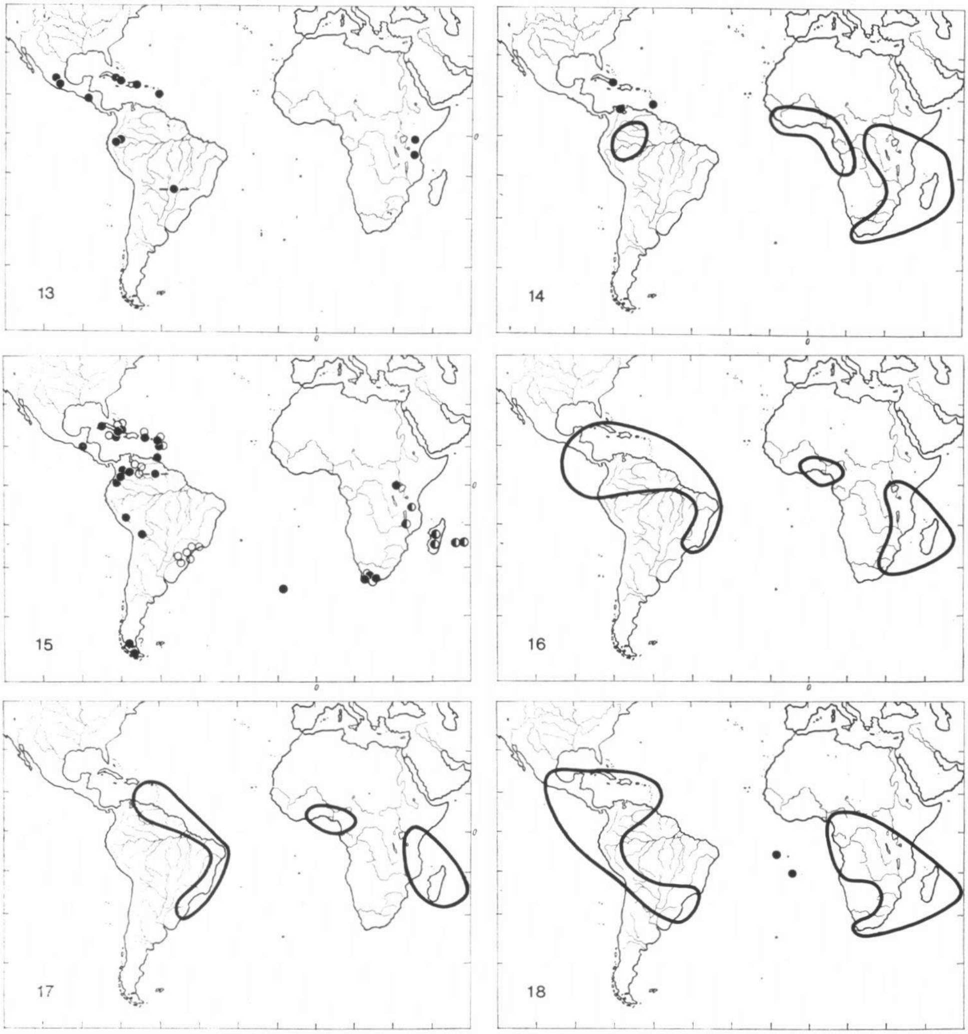

Plate III

Tropical montane species. 13. *Aphanolejeunea exigua* Evans. 14. *Arachniopsis diacantha* (Mont.) Howe. 15. *Kurzia capillaris* (Sw.) Grolle, full circle: var. *capillaris*; open circle: var. *verrucosa* (Steph.) Pócs; half circle: ssp. *stephanii* (Ren.) Pócs. 16. *Radula boryana* (Web.) Nees. 17. *Radula stenocalyx* Mont. 18. *Symphyogyna brasiliensis* Nees et Mont.

K. capillaris ssp. *capillaris* var. *verrucosa* (Steph.) Pócs l.c. There are transitions between *K. capillaris* and its ssp. *stephanii* and ssp. *capillaris* var. *verrucosa*.

Both varieties of *K. capillaris* ssp. *capillaris* are widespread in the montane forest belts of tropical America and Africa from Cuba to Tierra del Fuego and from Rwanda to Cape (more rare in Africa) and occur also on Tristan da Cunha. They descend also in submontane forests (near sea level in Cape) and on the other hand, occur near the forest line above 2000 m as well. They prefer the acidic, peaty floor of more open forest types, like *Pinus maestrensis* wood in Cuba or elfin forests in Africa. They occupy also tree bases, rotting logs and sometimes acidic rock surfaces.

K. capillaris is dioicous, asexual means of propagation are not known.

18. **Radula boryana** (Web.) Nees (Radulaceae) (Plate III/16)

Known from scattered localities in tropical America and Africa, and thus far most frequently found in East Africa and the adjacent islands. *R. boryana* is a submontane species occurring chiefly between 1000–2000 m (at least in continental Africa -- on islands often at lower altitudes), hence almost lacking in the vast rain forest regions of the Amazon and the Congo belts. The species has also been recorded for tropical Asia (CASTLE 1936) but according to YAMADA (1979) Asiatic records belong to other species.

R. boryana grows on trees or rock, rarely on soil, in moist submontane forests. The species is dioicous and seldom fertile. As means of asexual reproduction are unknown in this species, it is not likely, that long-distance dispersal currently operates successfully in this species. The possibility, however, that dispersal mechanisms were better for this species in the past should not be ruled out. On the other hand, this might be a case where former land connections and subsequent migration and evolutionary retardation on the species level were responsible together for the present disjunct distribution pattern.

19. **Radula stenocalyx** Mont. (Radulaceae) (Plate III/17)

A submontane, but apparently tropical coastal Afro-American species occurring scattered along the Atlantic and Indian ocean. The species is usually epiphyllous but, at least in tropical Africa, frequently corticolous as well (more often so than *R. flaccida*). Its American localities are poorly documented (mostly 19th century) but it occurs in humid montane forests, at 1400–2100 m in mainland East Africa and at lower altitudes (down to 500 m) on the East African islands and in West Africa. "It is much more montane than *R. flaccida* but the two species overlap in their altitudinal range" (JONES 1979: 502–503).

R. stenocalyx is dioicous (as all species of the sect. *Epiphyllae*) but produces perianths (and spores?) frequently; in addition it has copious gemmae production, as in *R. flaccida*.

20. **Symphyogyna brasiliensis** Nees et Mont. (Pelliaceae) (Plate III/18)

GROLLE recently (1980) proved its identity with the African *S. lehmanniana* Mont. et Nees. Widely distributed in the tropical mountains of both continents between the altitudes of 1500–3000 m, while in subtropical Brazil and Cape, and on the Galapagos islands descends near to the sea level. Most African localities are from the southern portion of that continent.

The species is always terrestric or rupicolous, occurring on wet ground, along trails, on streambanks, etc. In the Andes and in Southern Brazil the species is locally abundant. In the Andes and in Afroalpine localities occurs also in altimontane heath and in páramo vegetation even above the montane forest belt.

S. brasiliensis is dioicous and frequently fertile. Dispersal should be by spori as asexual means are as yet unknown. Its occurrence on young volcanic southern atlantic islands, as on Ascension and St. Helena as well as on the Galapagos islands indicates a capacity for long-range air dispersal.

21. Syzygiella concreta (Gott.) Spruce (Plagiochilaceae) (Plate IV/19)

Described by GOTTSCHE (1867) from Venezuela and Mexico; reported by INOUE (1966) also from SE Brazil (Caldas) and from Tristan da Cunha on the basis of type collections of *S. lingulata* Steph., and *S. tristaniana* S. Arnell, which were found to be conspecific with *S. concreta*. In Africa the species was recorded by VÁŇA et al. (1979) for Rwanda (mentioned also for Tanzania and Madagascar on the basis of unpublished records) and by BIZOT and PÓCS (1979) for Tanzania (Uluguru Mts.); it was collected also on Mt. Kenya. The African localities are all from montane altitudes (1900—2100 m), from the peaty ground of elfin forests and exceptionally, as epiphyllous (!). In Cuba it occurs on the bare lateritic soil of *Pinus maestrensis* forests at 1100 m altitude.

All species of *Syzygiella* are dioicous (INOUE 1966). In *S. concreta* perianths are known, but the sporophyte is as yet undescribed. Gemmae are also unknown. The record of this species from Tristan da Cunha, an oceanic island group of relatively recent origin (maximum 25 million years old) and located several thousands of miles from the mainland between S. Africa and S. America, may indicate that transoceanic air dispersal is operative in this species (cf. FRAHM 1982). According to pteridological evidence (MANTON and VIDA 1968, TRYON 1966) immigrants "have come mainly though not entirely from the general direction of South America" by long range air dispersal, then in the case of ferns, speciation took place mainly by polyploidization.

22. Diplasiolejeunea pellucida (Meissn.) Schiffn. and Diplasiolejeunea albifolia (Tayl.) E. W. Jones (Lejeuneaceae) (Plate IV/20)

Closely allied vicariant species pair sometimes treated as conspecific, although they are distinct, having constant differences in the length and shape of their lobule teeth.

D. pellucida occurs from the lowland to the montane forest belt of the Caribbean region and northern South America, between 200 and 1750 m altitudes, while *D. albifolia* seems to be more montane, occurring except for its type locality in the lowland forest belt of Nigeria between 1370 and 2100 m in the montane forests of East Africa, where it was first collected by PÓCS (BIZOT and PÓCS 1974: 410). From Mauritius it is mentioned already by EVANS (1912: 214) under *D. pellucida* based on the old collection made by RODRIGUEZ.

Both species are obligate epiphyllous in rain forests, dioicous, with discoid gemmae common on the leaf surface. *D. pellucida* shows variability in the occurrence of a malleiform apical lobule tooth, while *D. albifolia* in East Africa has a variety with a several cells broad hyaline margin.

23. Jungermannia amoena Lindenb. et Gott. and Jungermannia borgenii Gott. (Jungermanniaceae) (Plate IV/21)

J. amoena is a montane species occurring at many localities in south-eastern Brazil and having scattered localities also in the Peruvian and Colombian Andes and one-one localities in Mexico and Jamaica. The species grows on soil at higher elevations (800–2500 m, VÁŇA 1974). The African vicariant, *J. borgenii*, is the commonest African *Jungermannia*, recorded from Nigeria, Cameroon, and from Uganda and Kenya to South Africa, incl. Madagascar and the Mascarenes. It grows on places ecologically similar to the above, on soil and on bare, often on wet rocks, at more or less open places between 1000 and 3300 m (Mt. Elgon), seldom at 400 m (Rep. Congo).

Both species are dioicous and produce spores in most cases.

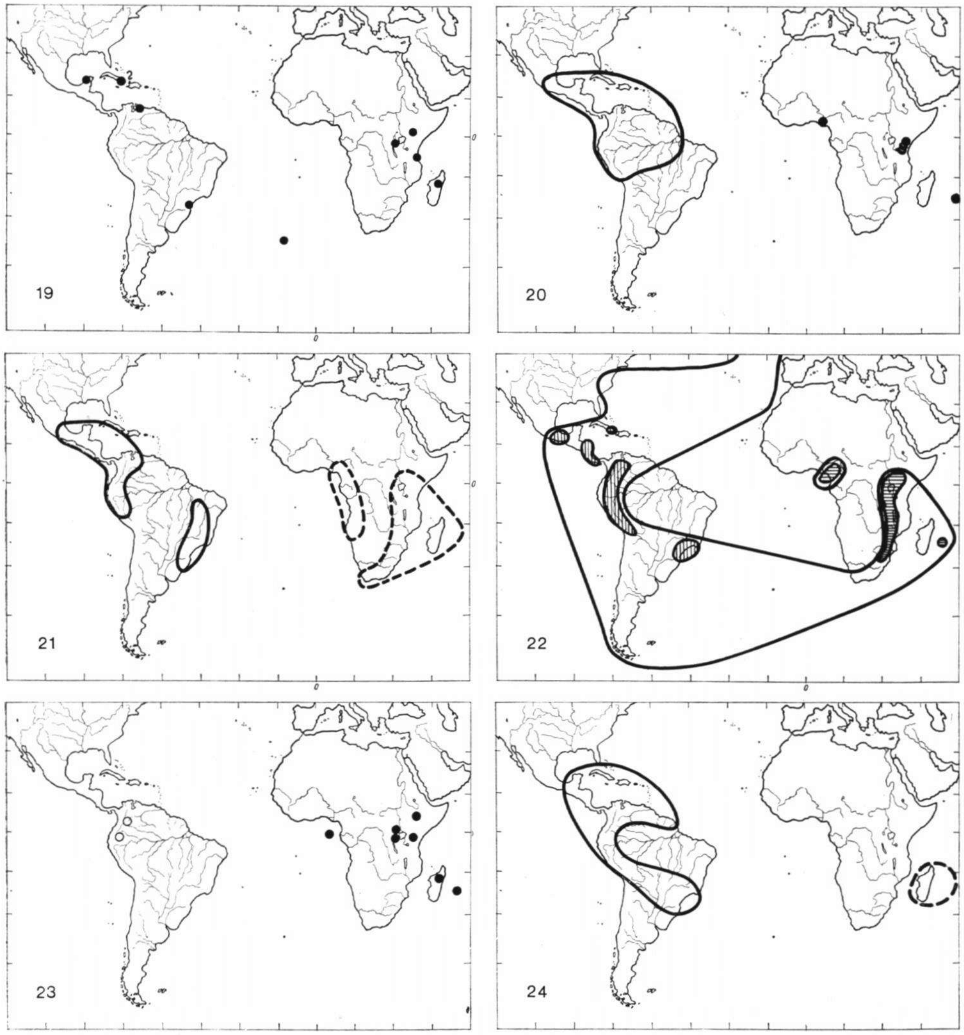

Plate IV

Tropical montane species. 19. *Syzygiella concreta* (Gott.) Spruce. 20. *Diplasiolejeunea pellucida* (Meissn.) Schiffn. (line) and *Diplasiolejeunea albifolia* (Tayl.) E. W. Jones (dots). 21. *Jungermannia amoena* Lindenb. et Gott. (continuous line) and *Jungermannia borgenii* Gott. (broken line). 22. *Leptoscyphus amphibolius* (vertically) and *L. infuscatus* (horizontally striped areas). The continuous, solid line marks the area of the genus *Leptoscyphus* Mitt. (total distribution of 24 species). 23. *Syzygiella manca* (Mont.) Steph. (open) and *S. geminifolia* (Mitt.) Steph. (full circles). 24. *Bryopteris* Nees. Continuous line: 6 neotropic species, broken line: *B. gaudichaudii* Gott.

24. **Leptoscyphus amphibolius** (Nees) Grolle and **Leptoscyphus infuscatus** (Mitt.) Jones (Geocalycaceae) (Plate IV/22)

These two vicariant species form the section *Physoscyphus* (GROLLE 1962: 51).

L. amphibolius represents a relatively common species growing on rotten logs, rarely on sandy soil in the mountain forests of the Andes from the southern part of Mexico to Bolivia; it is known also from the Sierra Maestra in Cuba and from mountains of south-eastern Brazil. The species was collected at elevations 1000-3000 m (GROLLE 1962, FULFORD 1976, VÁŇA ined.).

The African vicariant, *L. infuscatus*, is known from the montane rain forests of Fernando Poo and Mt. Cameroon in West Africa and has several localities in East Africa in Ethiopia, Zaire, Mt. Muhawura, Mt. Ninagongo, Mt. Kilimanjaro, Ruwenzori Mts., Malawi and in the Inyanga Mts. in Zimbabwe; also on Réunion island (GROLLE 1962, BIZOT and PÓCS 1974). Questionable is a locality in Java, based on the data of the label of a *Leptoscyphus motleyii* Mitt. specimen (conspecific with *L. infuscatus*), where a probably label change is at hand. No other collection of any *Leptoscyphus* is known from Asia (cf. also GROLLE 1962).

Both species are dioicous and produce sporophytes. Gemmae are unknown.

25. **Syzygiella manca** (Mont.) Steph. and **Syzygiella geminifolia** (Mitt.) Steph. (Plagiochilaceae) (Plate IV/23)

S. manca is an Andean species known from the northern part of South America (Ecuador, Colombia — cf. INOUE 1966), while its African vicariant, *S. geminifolia*, was treated by INOUE (l.c.) as two species (*S. geminifolia* and *S. ruwenzorensis* Steph.). This concept was criticized by JONES (1976) and the two species were shown to be identical by VÁŇA et al. (1979). Recently, *S. geminifolia* has become known from scattered localities in S. Tomé, Ethiopia, Ruwenzori, Rwanda, Mt. Kilimanjaro, Madagascar and Réunion (VÁŇA, in prep.). The report of *S. geminifolia* from Brazil (INOUE 1966) is erroneous; the material belongs to the broad-leaved form of *S. perfoliata* or *S. concreta*.

S. manca grows on rocks in the montane belt (about 2000–2500 m), while *S. geminifolia* is known from trees and rocks in montane rain forests at 1650–2000 m (reaching 3300 m in Ruwenzori Mts.).

Both vicariants are dioicous and known with one exception only in sterile conditions (STEPHANI 1902, described sporophyte of *S. manca*). Gemmae are unknown.

26. **Bryopteris** Nees (Lejeuneaceae subfam. Bryopteridioideae) (Plate IV/24)

A clearly defined genus representing a monotypic subfamily, with 6 species in tropical America (*B. diffusa*, *B. filicina*, *B. flaccida*, *B. fruticulosa*, *B. liebmanniana* and *B. trinitensis*) and a 7th species on Madagascar: *B. gaudichaudi* (STOTLER and CRANDALL-STOTLER 1974). In addition, the neotropical *B. trinitensis* has been reported from several scattered palaeotropical localities, but all these are very old and poorly documented and therefore for the moment can hardly be accepted (STOTLER and CRANDALL-STOTLER, l.c.). The alleged Nepal record of *B. trinitensis* (STOTLER and CRANDALL-STOTLER l.c.) was recently shown, by MIZUTANI (1979), to represent misidentified *Ptychanthus striatus*.

If the occurrence of *Bryopteris* in Madagascar is correct (there are only a few 19th century records for *B. gaudichaudii*, notwithstanding active collecting on Madagascar during recent years by ONRAEDT, TIXIER a.o.), then the distribution of *Bryopteris* may be compared with that of *Symbiezidium* and other "peri-Afroamerican" elements, indicating a Gondwanic origin for the genus. Potential habitats should be plentiful for *Bryopteris* on the African mainland! Even on the old crystalline blocks of Eastern Tanzania, where floristic affinities to Madagascar are close (Pócs 1974), neither *Bryopteris*, nor *Symbiezidium* have been found.

The Madagascan *B. gaudichaudii* is apparently a close relative and vicariant of the common neotropical *B. diffusa*; morphologically these two species seem clearly separated from the rest of the genus and probably represent a proper section, with its own evolutionary history.

In tropical America the genus is very common, representing epiphytes in mesic to moist submontane forests, both primary and degraded. *Bryopteris* disperses there by spores, and vegetatively probably by flagelliform branches. Its species are either autoicous or dioicous.

I.c. Tropical alpine element

27. Andrewsianthus jamesonii (Mont.) Váňa, comb. nova (Jungermanniaceae) (Plate V/25)

Basionym: *Jungermannia jamesonii* Mont., Sylloge Gen. Spec. Crypt., p. 60 (1856).
Lectotype: Ecuador, "Quito, M. Jameson, cum *Calypogeia trichomanis*"; PC-Mont.!; isotype: PC-Mont.!
Syn. nov.: *Jungermannia achroa* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 514 (1885). Holotype: Ecuador, Andes Quitenses, Mt. Tunguragua, 2200 m, R. Spruce: MANCH (not seen); isotype: G!
Cephaloziopsis achroa (Spruce) Schiffn. in Engler, Prantl, Nat. Pflanzenfam. 1 (3): 85 (1893)
Sphenolobus achrous (Spruce) Steph., Spec. Hep. 2: 174 (1902)
Andrewsianthus achrous (Spruce) Schust., Nova Hedwigia 8: 207 (1964)
Lophozia kilimanjarica S. Arnell, Ark. Bot. 3 (16): 539 (1956). Holotype: Tanzania, Mt. Kilimanjaro, O. Hedberg 1363d; UPS!
Andrewsianthus kilimanjaricus (S. Arnell) Grolle et Váňa, J. Hattori Bot. Lab. 48: 228 (1980)

Jungermannia jamesonii Mont. (type from Ecuador) is probably the earliest name for *A. kilimanjaricus*, which was treated in detail by Váňa (1980), who demonstrated the Afro-American distribution of the species. The lectotype and isotype specimens in PC-Mont. (probably the only available type material) consist only of some stems without branching, but the other characteristics (leaf form, cell size and form etc.) exclude *Lophozia incisa* (Schrad.) Dum., which also occurs in the same area and was mostly confused with *A. jamesonii.*

Jungermannia achroa (= *A. achrous*) was known only from type collection, the holotype of which was not obtainable from MANCH (missing?). The only isotype material available (G, Stephani herbarium) consists of a few poorly developed male stems with strongly unequal leaf lobes and reduced leaf margin dentation (male bracts!); the description of such plants gave a basis for the distinguishing characteristics of this species cited in Schuster (1964, 1966).

Schuster (1978) described *Lophozia incisa* ssp. *austrigena* Schust. from Venezuela. The type material is not available, but this taxon is probably also conspecific with the present species.

The known distribution of *A. jamesonii* was published by Váňa (1980); recently many new localities were added from Ecuador (Carchi, Gradstein et al. 3427 and the two above-mentioned type specimens), Colombia (new localities from Cundinamarca, Boyacá, Meta, Tolima) and Mexico (Oaxaca, Sierra Juárez, A. J. and E. Sharp 9895-a). *A. jamesonii* is restricted both in East Africa and in the Andes to high-montane and alpine localities, between 2000 and 4000 m, but extending up to 4750 m on summit rocks of Mt. Pichincha near Quito, Ecuador. The species is terrestric or saxicolous and sometimes grows together with *Lophozia incisa*, which it resembles. The habitat is montane mossy forest, Ericaceous heath, subpáramo or páramo vegetation.

It is dioicous but frequently fertile. Within *Andreusianthus* (pantropical-circum-subantarctic genus of ca. 20 species) *A. jamesonii* has probably the best capacity for dispersal as it is the only species which develops gemmae besides spores. This may possibly explain why *A. jamesonii* is the only macro-disjunct species within the genus.

28. Gymnocoleopsis multiflora (Steph.) Schust. (Jungermanniaceae) (Plate V/26)

An apparently rare, tropic-alpine species known from the Andes (Bolivia, Peru, Colombia — unpublished records from Sierra Nevada del Cocuy and Risaralda —, and Venezuela) and in Africa from Zaire (Váňa 1982). Its altitudinal range extends from 3500 m (Zaire: Karisimbi) to 4400 m (Bolivia, near Tunarisca). It grows on humid, boggy ground among higher plants and on moist rocks.

Schuster (1966) separated *Gymnocoleopsis* [as a monotypic genus, the position of *G. cylindriformis* (Mitt.) Schust. from Kerguelen is not clarified] from *Gymnocolea* on the basis of the persistent perianths (caducous in *Gymnocolea*), and described the sporophyte. *G. multiflora* is autoicous but often sterile. Nevertheless, dispersal by spores should be possible.

29. Herbertus subdentatus (Steph.) Fulf. (Herbertaceae) (Plate V/27)

(data kindly provided by G.B. A van Reenen, Utrecht)

H. subdentatus is known in tropical America between 3100 and 4350 m in the montane and alpine zones of the Andes, from Mexico to Bolivia, and from the summit of Mt. Roraima (Fulford 1963, van Reenen 1982). It is a very variable species (van Reenen 1982) but there are sufficient morphological traits to separate it from other tropical American species, such as the numerous ventral intercalary flagelliform branches, the imbricate and appressed, secund leaves, the broadly V-shaped leaf sinus and the convex vitta which is especially notable in the underleaves. The species is mainly restricted to regions with heavy precipitation (e.g. above 3000 mm in Tanzania) and high atmospheric humidity.

The same habitat and morphological characters apply to a number of *Herbertus* specimens recently examined by the above author from Africa and identified as *H. subdentatus*. These specimens are from the collections made by T. Pócs on Mt. Kilimanjaro and the Southern Highlands of Tanzania, between 1700–3300 m. Strikingly, about half of the collections contain sporophytes while these are seldomly encountered in tropical American populations. Following Grolle (1978), the African material of *H. subdentatus* belongs in the "*H. capensis* complex", but the name *Herbertus subdentatus* can be used safely here since all the names of species assigned to this complex by Grolle (1978) are of younger date.

A preliminary comparison of *H. subdentatus* with species from other regions revealed a rather close relationship to the holarctic *H. aduncus* (which, however, remains distinct on the species level, cf. van Reenen 1982), and a very close similarity to the atlantic European *H. borealis* Crundw. Based on examination of the type (GL), kindly provided by Dr. Crundwell, it appears that the only morphological difference between *H. subdentatus* and *H. borealis* is in the position of the leaves, which are more spreading in *H. borealis*. According to Miller (cited by Crundwell 1970) *H. borealis* is very near to the Asiatic *H. himalayana* (Steph.) Chopra. These further relationships might have considerable taxonomic and phytogeographical

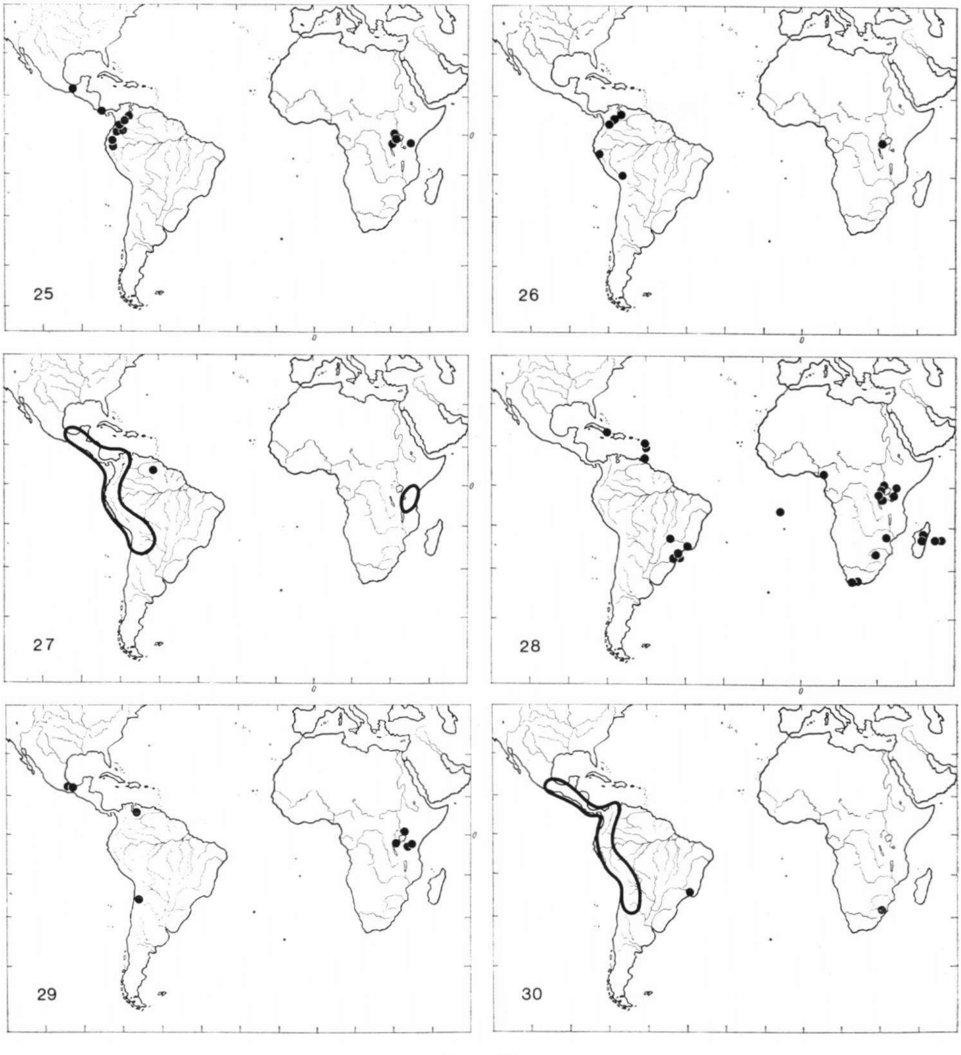

Plate V

Tropical alpine species. 25 *Andrewsianthus jamesonii* (Mont.) Váňa. 26. *Gymnocoleopsis multiflora* (Steph.) Schust. 27. *Herbertus subdentatus* (Steph.) Fulf. 28. *Isotachis aubertii* (Schwaegr.) Mitt. 29. *Marsupella africana* Steph. ex Bonner. 30. *Stephaniella paraphyllina* Jack.

implications. Yet, it is too early to draw conclusions based on these preliminary observations and therefore it seems better to treat *H. borealis* as a separate species pending further study.

30. Isotachis aubertii (Schwaegr.) Mitt. (Isotachidaceae) (Plate V/28)

Váňa (1982) showed that *I. aubertii* is a common, montane to tropic-alpine species in Africa where it occurs at 2000–4500 m in the East African mountains and on Mt. Cameroon, at 1500–2000 m in South Africa and at lower altitudes on the islands (on Réunion even at 400 m!). The species is rather polymorphic like other species of this genus and has many African synonyms.

In tropical America the species was reported by HATCHER (1961) from two areas: montane SE Brazil (Itatiaya) and scattered localities in the West Indies reaching to Sierra Maestra in Cuba. As HATCHER's monograph of *Isotachis* (HATCHER 1961) proved unsatisfactory at least for Africa (VÁŇA 1982) it remains to be proved whether the absence of *I. aubertii* from the main mountain ranges of tropical America is correct. The careful study of many collections from the South American Andes (VÁŇA, GRADSTEIN) agree with HATCHER's (1961) results; no specimen of *I. aubertii* from the Andes was found.

All species of *Isotachis* are dioicous but sporophytes may be found under favourable (wet) conditions. The occurrence of *I. aubertii* on the young volcanic, oceanic island of Ascensión in the middle of Atlantic Ocean between Africa and America indicates the possibility of recent long-range dispersal for this species.

31. **Marsupella africana** Steph. ex Bonner (Gymnomitriaceae) (Plate V/29)

Syn. nov. *Acolea africana* Steph., Spec. Hep. 6; 77 (1917). Lectotype sensu GROLLE in sched. 1963: Kilimanjaro, C. UHLIG s.n., G-10874 !, isolectotype S !

Gymnomitrion africanum (Steph.) Horik., Acta Phytotax. Geobot. 13: 212 (1943)

Marsupella chilensis Steph. ex Bonner, Candollea 14: 254 (1953). Holotype; Chile, GAY s.n., G-10880 !, isotype PC

Marsupella hedbergii S. Arnell, Ark. Bot. 3 (16): 544 (1956). Holotype; Tanzania, Mt. Meru 3400 m, O. HEDBERG 2369b, UPS !, isotype S !

Marsupella subquadrata Steph. in sched. et Icones ined. Type: Kilimanjaro, Garanga Bach, 1901 C. UHLIG, G-15048 !

A tropical alpine species which was known from the high mountains of East Africa (Mt. Kilimanjaro, Mt. Meru, Mt. Karisimbi and Mt. Elgon). In the meantime it has become known from the American Cordilleras as well (Mexico: Mt. Popocatepetl, Mt. Nevado de Toluca, Mt. Ixtaccihuatl; Venezuela: Merida; Chile).

In Africa the species occurs in rather xerophytic alpine and subalpine vegetation types, in rock crevices usually in the *Philippia* zone but on Mt. Kilimanjaro in the alpine tussock and *Helichrysum* semidesert zones (3600–4500 m). In tropical America it grows in alpine grassland on mesic basalt outcrops; in Mexico even on active volcanoes.

The species is dioicous and usually sterile. The dispersal via stem fragmentation (as is postulated for *Stephaniella* occurring among similar dry-alpine environmental conditions) is problematic, but should be possible.

32. **Stephaniella paraphyllina** Jack (Gymnomitriaceae) (Plate V/30)

A tropical alpine species distributed all along the Andes from northern Argentina to Colombia and known also from Costa Rica and Mexico, ranging in altitude from ca. 3000–4500 m. In addition, there is a single record from Africa: Natal, Drakensbergen, 3300 m. GROLLE (1969), who mapped the species, considered its distribution as showing a "subantarktische Beziehung". Since the species occurs only in tropical and southern subtropical regions, and is very common in the northern Andes (páramo region), this qualification is less suitable. We would rather qualify it as a tropical alpine species and would predict it to turn up once at the high levels of the East African mountains as well.

The genus, as a whole, is alpine Afro-American with 5–6 species in the Andes (SCHMITT and WINKLER 1969). *S. paraphyllina* is far the most common species among them and also the only species known from Africa. All species are strongly specialized xeromorphic, adapted to open soils in the alpine environment exposed to extreme climatic conditions (radiation, desiccation, frost).

The species is autoicous or dioicous, but apparently sporophytes are rare. Asexual means of dispersal in *Stephaniella* remain unknown, but we would assume that stem fragments of the worm-like plants could be carried away by winds when the open soils on which they grow dry out entirely.

33. **Colura ornithocephala** Herz. and **Colura kilimanjarica** Pócs et S. J.-Ast (Lejeuneaceae) (Plate VI/31)

A vicariant species pair belonging to the very conservative Section *Oidocorys*. All members of this group are distributed in the dissected parts of former Gondwanaland. Their taxonomy, phytogeographical relations were discussed in details by JOVET-AST (1980), who is in the opinion, that the distribution of these closely related species or their ancestor could happen to a long distance before the continental drift, nearly 100 million years ago. Since that time very little speciation took place. Anyway, the occurrence of the African species on a young tertiary volcano indicates that *C. kilimanjarica* had to survive at an other place and that this locality is the result of more recent migration. Both species are tropical subalpine, living in subpáramo-like vegetation at 2900–3800 m altitude, and are still known from very few collections only [*C. kilimanjarica*: only type collection; *C. ornithocephala*: Ecuador (type) and Colombia, Risaralda (leg. AGUIRRE et GRADSTEIN)].There is a doubtful record of *C. ornithocephala* from the Galapagos islands as well (BARTRAM and ARNELL 1961).

C. ornithocephala seems to be dioicous, while *C. kilimanjarica* is monoicous. Asexual way of reproduction was not observed.

34. **Gongylanthus liebmannianus** (Lindenb. et Gott.) Steph. and **G. scariosus** (Lehm.) Steph. (Arnelliaceae) (Plate VI/32)

A vicariant species pair of Afro-American montane-alpine, terrestric liverworts. *G. liebmannianus* lives in the high mountain areas of tropical America, ranging from ca. 3200 up to 4300m (Mexico, Central America and the Andes). Occasionally is found at lower elevation, in the upper forest zone, on roadsides (e.g. Itatiaya in SE Brazil). In Colombia it is mainly a páramo species (GRADSTEIN et al. 1977: 397) extending up to the superpáramo in the Sierra Nevada del Cocuy. It grows often associated with *Stephaniella paraphyllina*, but *G. liebmannianus* prefers more shadow and humidity than *Stephaniella*. It is found sometimes even in Sphagnum bogs. One locality is known from the humid, upper Andean *Weinmannia* cloud forest.

The related *G. scariosus* is known only in subtropical South Africa, from the Cape peninsula and from the 1623 m high Anysberg near Ladysmith (ARNELL 1963). We do not know much about its ecology.

Probably both species are dioicous. The marsupium of *G. liebmannianus* is 3 mm, while that of *G. scariosus* is only 1.5 mm long (fide descr. STEPHANI 1906 and S. ARNELL 1963). ARNELL (l.c.) observed the sporophytes and spores of *G. scariosus* as well. According to him its spores are large, collapsing when dry (25–29 μm in diam.) and "evidently dispersed by wind". Sporophytes of the American plant are not known.

35. Lethocolea glossophylla (Spruce) Grolle and Lethocolea congesta (Lehm.) S. Arnell (Acrobolbaceae) (Plate VI/33)

Lethocolea glossophylla is a high-Andean species, occurring sporadically in Colombia, Ecuador, Peru (? and Bolivia). *Lethocolea congesta* (Lehm.) S. Arnell is known from the high mountains of East Africa (Mt. Elgon, Ruwenzori Mts., Mt. Muhawura, Mt. Bysoke, Mt. Meru, Kilimanjaro Mts. and Rungwe Mts.), from South Africa (Transvaal, Natal, Cape), from the islands of Réunion, Inaccessible and Tristan da Cunha.

The ecology of the two species seems rather similar. *Lethocolea glossophylla* occurs mostly on steep, shaded, moist earth and rocks in the upper montane to alpine zone (2700–3750 m in Colombia according to GRADSTEIN and HEKKING 1979: 119), while *L. congesta* is known from montane forest and subpáramo-like vegetation, as subalpine *Philippia* moorland on earth and on wet rocks near watercourses, between 2250 and 3800 m according to ARNELL (1956), BIZOT and PÓCS (1974, 1979). It occurs much lower in South Africa, on Réunion (1800 m fide ARNELL) and at 80–1200 m on Tristan da Cunha (ARNELL 1958).

L. glossophylla is dioicous, while *L. congesta* probably paroicous. The sporophyte is known only in *L. glossophylla*. Main type of dispersal in both species is by disciform gemmae. The occurrence of the African species on Tristan da Cunha seems to prove its long range air dispersal ability from East to West. However, the taxonomic relationship of this species pair needs further study.

II. SUBTROPICAL-MEDITERRANEAN AFRO-AMERICAN ELEMENTS

Altogether only two species belong here, which cannot be classified elsewhere; even the two represent different types of distribution:

II.a. Southern subtropical element

36. Sphaerocarpos stipitatus Bisch. ex Lindenb. (Sphaerocarpaceae) (Plate VI/34)

With *S. mucilloi* Vianna from Southern Brazil *Sphaerocarpos stipitatus* is the only representative of the genus known with certainty from the southern hemisphaere (there are uncertain records of *S. texanus* as well). The genus is a characteristic element of dry subtropical-mediterranean regions and the distribution of *S. stipitatus* seems to fit that pattern very well. There are only three localities known thus far (PROSKAUER 1954, ARNELL 1963): Chile, Valparaiso, leg. BERTEN 1829 (not rediscovered since in America !) and two more recent localities in S. Africa, where it was found on muddy, temporarily moist riverbanks. More intensive collecting at the right places and at the right moment of the year should reveal additional localities for this poorly known, disjunct Afro-American species.

All *Sphaerocarpos* species are dioicous and disperse by spore tetrads (over 100 μm in diameter !). It is unlikely that the large tetrads are carried by wind, but dispersal by birds seems not unlikely in view of its occurrence on the shore of ponds and rivers.

II.b. Widely distributed element

37. Exormotheca pustulosa Mitt. (Exormothecaceae) (Plate VI/35)

According to BISCHLER (1976) *E. pustulosa* is the most widespread species of this subtropic-mediterranean genus to which about 7 species have been attributed (cf. also SCHIFFNER 1942). *E. pustulosa* ranges from the western European mediterranean region to southern,

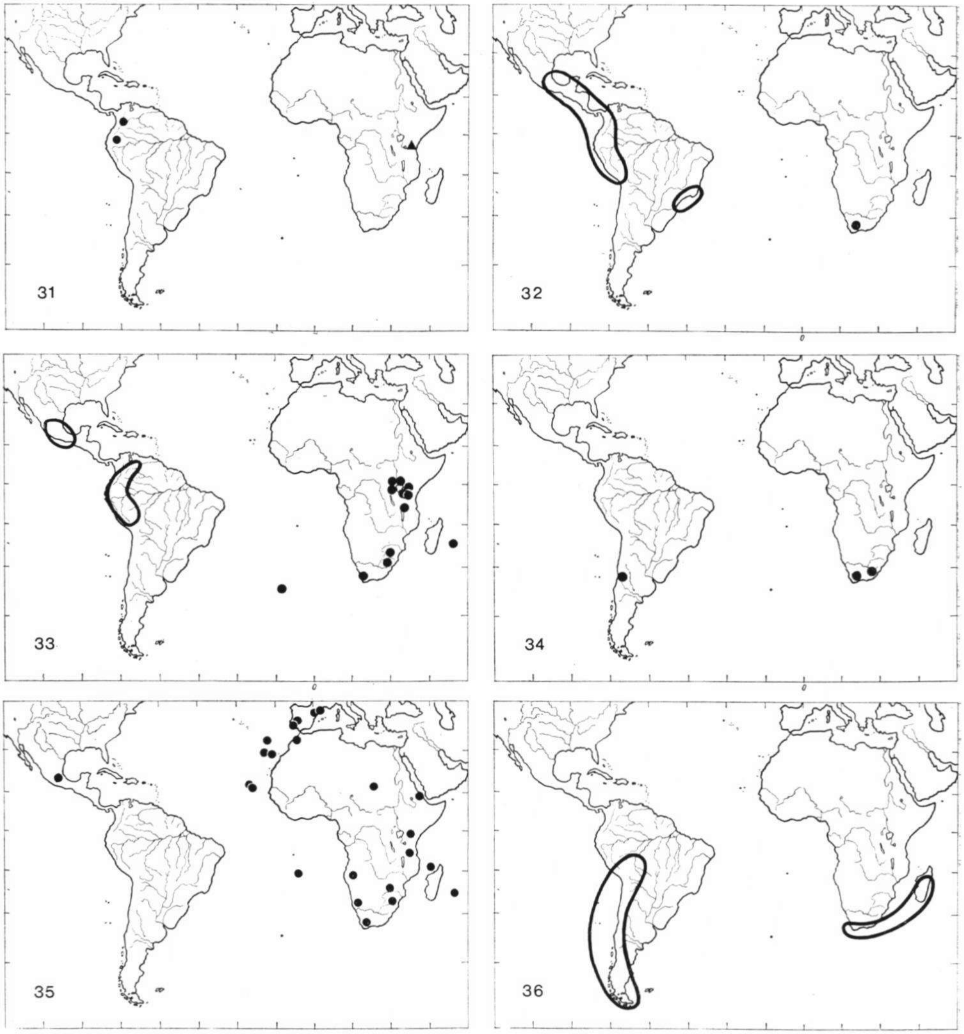

Plate VI

31–33: Tropical alpine. 34–35: Subtropical-Mediterranean and 36: Southern temperate species penetrating in tropical mountains. 31. *Colura ornithocephala* Herz. (dots) and *C. kilimanjarica* Pócs et S. J.-Ast (triangle). 32. *Gongylanthus liebmannianus* (Lindenb. et Gott.) Steph. (line) and *G. scariosus* (Lehm.) Steph. (dot). 33. *Lethocolea glossophylla* (Spruce) Grolle (line) and *L. congesta* (Lehm.) S. Arnell (dots). 34. *Sphaerocarpus stipitatus* Bisch. ex Lindenb. 35. *Exormotheca pustulosa* Mitt. 36. *Heteroscyphus integrifolius* (Lehm. et Lindenb.) Fulf.

subtropical Africa, with localities also in tropical Africa near the coasts and on islands, especially those of the Atlantic Ocean. In tropical America a single recent locality is known, from Mexico (Düll in Bischler 1976: 771). The species is always terrestric (incl. soil covered rocks) and occurs in habitats only temporarily moist. Microclimate and substrate conditions were described by Bischler (l.c.). It has probably been overlooked, being almost invisible during dry seasons and its range may be larger, especially in the temporarily dry tropics, than is presently known. In tropical Africa it grows in xerophytic, rocky Velloziaceae bush or on the ground of miombo woodland (BIZOT and PÓCS 1979; 236), while the Mexican locality is from the soil of Mexico City Botanic Garden (R. DÜLL and R. GROLLE pers. comm.), which occurrence suggests the possibility of introduction. It occurs from sea level to 2300 m according to latitude.

E. pustulosa is autoicous (which fits its large range) and disperses by spores. In view of their large size (50–65 μm) wind dispersal should be less likely in this species. Vegetative reproduction is unknown.

III. TEMPERATE-SUBANTARCTIC AFRO-AMERICAN ELEMENTS

As argued by ENGEL (1978), this group of species is often unjustifiedly called "subantarctic" as their main range is in the southern temperate region following the definitions of recent phytogeographers (e.g. WACE, GREENE). Most of them penetrate northwards, some even through the tropics into the northern temperate region. Based on this criterium two elements can be distinguished:

III.a. Southern temperate element, with sporadic penetration into tropical mountains

The phenomenon, that southern temperate elements, often with Gondwanalandic origin, occur northwards in tropical mountains, is well known among phanerogams and widely discussed, especially in the case of páramo vegetation (e.g. CLEEF 1978). This type of migration was promoted by the upheaval and related climatic changes in the south-north oriented Andes (VAN DER HAMMEN et al. 1973), but in some cases occurred also in East Africa, where southern temperate elements penetrate in the more isolated high mountains (e.g. *Clasmatocolea vermicularis*, BIZOT and PÓCS 1974: 396). The phenomenon can be explained the same way. Even if the migration route from South to East Africa is not so continuous, a chain of montane areas can act as stepping stones, especially if we take in account the much more continuous and more depressed forest belts during pluvial periods, compared to the present (cf. COETZEE 1964, 1967).

38. **Clasmatocolea vermicularis** (Lehm.) Grolle (Geocalycaceae)

Clasmatocolea vermicularis was discussed in details and mapped by GROLLE (1960) and served also for FULFORD (1963) as an example for the above discussed distribution pattern. According to the very detailed data of GROLLE (l.c.) and to the new unpublished records of GRADSTEIN et al. it grows on different substrates, e.g. in Peru from 1300 m altitude, up to 4400 m in Bolivia; near sea level in temperate South America and on the subantarctic islands, from sea level to 700 m in Tristan da Cunha, from 300 to 1000 m in South Africa, finally at 1410 m in the highlands of Zimbabwe.

The above records were supplemented by new data from the high mountains of East Africa, as from the Rungwe Mts. in southern Tanzania, where *C. vermicularis* grows on earth banks (roadcut in volcanic ash) on the foot of Mt. Kyejo, a recent volcano, at 1725 m altitude (Bizot and Pócs 1974; 401) and from Rwanda: Gikungu and Burundi: Mt. Manga-Mugongo, Sikuvyaye and Nyakazu, collected by De Sloover in montane forests, grasslands, on wet roadcut surface and on humid rocks, from 1700 to 2300 m altitudes (Váňa et al. 1979).

The species is dioicous and produces spores of 16–20 μm diameter. Gemmae were not observed.

One part of the East African localities (roadcut surfaces on young volcanic soil) suggests the possibility of easy dispersal over short distances, step by step way.

39. **Heteroscyphus integrifolius** (Lehm. et Lindenb.) Fulf. (Geocalycaceae) (Plate VI/36)

According to Fulford (1976) the species occurs in the southern Andes (Patagonia, Chile, Tierra del Fuego) reaching to Peru and Bolivia and also Juan Fernandez. Fulford (l.c.) also reported this species from Madagascar (type of *Lophocolea integrifolia* Steph.) and from South Africa, although Arnell (1963) did not mention this species.

H. integrifolius is monoicous but sporophytes remain undescribed and no asexual mean of reproduction is known.

40. **Hyalolepidozia bicuspidata** (Massal.) S. Arnell ex Grolle (Lepidoziaceae) (Plate VII/37)

The species is known from the southernmost edges of both continents and from Tristan da Cunha, from wet rock faces and from tree fern stems, among other hepatics according to Arnell (1958) and Fulford (1968), from sea level to about 700 m altitude.

It is dioicous and reproduces by spores. Both the small spores (12 μm in diameter) and the numerous thin stolons, which easely brake off, seem to be adequate means of dispersal.

41. **Lepicolea ochroleuca** (Spreng.) Spruce (Lepicoleaceae) (Plate VII/38)

Lepicolea ochroleuca was originally described from South Africa (Cape) but is more widely distributed in Latin America, where it is known from two disjunct areas; the temperate-subantarctic tip of South America (Patagonia — Tierra del Fuego) where it grows near the sea level, and from the tropical mountains of Central America (Mexico to Honduras, Fulford 1963), where it grows above 1600 m. Surprisingly, the species is not known from intermediate Andean regions, although there are unconfirmed, old records from Bolivia. As the species occurs on cool forest soil, over rock and on tree bark, there seems no reason, why it would be disjunct in the Latin American mountain range.

Lepicolea ochroleuca belongs to a putative primitive genus of liverworts, all species of which are dioicous. Female plants have been found occasionally but the sporophyte remains undescribed in this species. Asexual means of reproduction are unknown. Its present distribution and the lack of dispersal agents seem to suggest its relict character, a Gondwanalandic origin before its dissection and a secondary migration northwards up to Mexico, as it was suggested already by Fulford (1963).

42. **Leptoscyphus expansus** (Lehm.) Grolle (Geocalycaceae) (Plate VII/39)

The genus *Leptoscyphus*, as delimited by Grolle (1962), is mainly Afro-American in distribution (see also map 22) and has two centers of diversity: the tropical Andes and southern

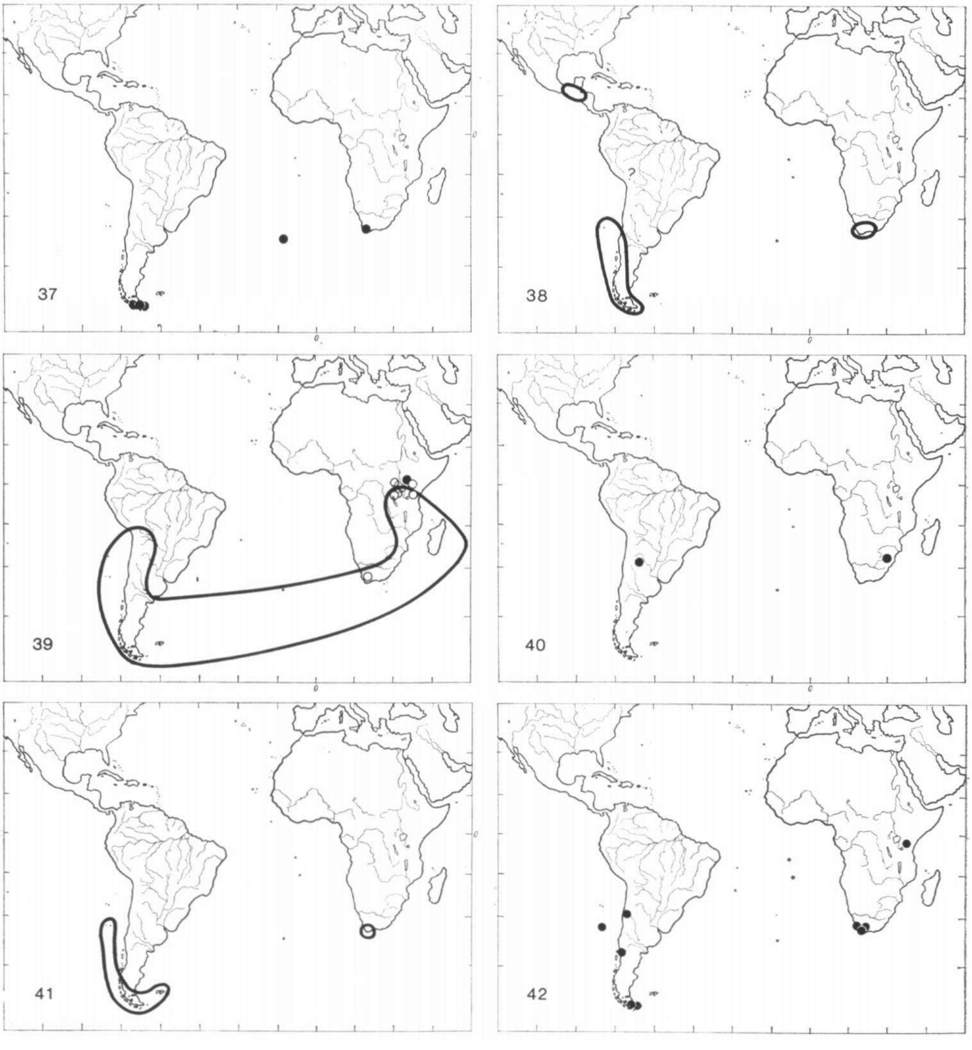

Plate VII

Southern temperate species with sporadic penetration into tropical mountains. 37. *Hyalolepidozia bicuspidata* (Massal.) S. Arnell ex Grolle. 38. *Lepicolea ochroleuca* (Spreng.) Spruce. 39. *Leptoscyphus expansus* (Lehm.) Grolle (solid line and black dot) and *L. hedbergii* (S. Arn.) Schust. (open rings). 40. *Lophozia argentina* (Steph.) Schust. 41. *Schistochila alata* (Lehm.) Schiffn. 42. *Tylimanthus limbatus* Steph.

tip of S. America and adjacent subantarctic islands. 19 species are known from tropical America (FULFORD 1976), only 6 species are growing in the African continent. Recently one undescribed species was discovered by R. MUES in New Zealand (genus named by GROLLE and VÁŇA), which seems to be closely related to *L. expansus*, but not conspecific. *L. expansus* is the only species occurring in each of the two continents. It is temperate-subantarctic ranging in South America from Tierra del Fuego to Bolivia (Comarapa, 2500 m) and in Africa from

Cape to Shaba (VANDEN BERGHEN 1978), Rwanda (VÁŇA et al. 1979), and to Mt. Elgon, 3000 m altitude (coll. AGNEW, det. GROLLE, ined.). It is furthermore known from Madagascar and Mascareignes and from various subantarctic island groups (S. Georgia, Falkland I., Staaten I., Cape Horn), from Gough I. and Tristan da Cunha.

In southern S. America it is by far the most common species of the genus, growing extensively on soil, rotten logs and stumps in the deciduous and drier region in the evergreen forests (ENGEL 1978), where it is rather xerophytic. Of particular interest is its occurrence on tidal rocks in southern Chile where it tolerates salt water spray. The implications of this habitat for possible dispersal by sea currents were discussed by ENGEL and SCHUSTER (1973).

In tropical African mountains the species occurs in montane forests at ca. 2000—2500 m altitude. A closelv related. robust vicariant. *L. hedbergii* (S. Arn.) Schust. occurs above 3200 up to 4000 m in the alpine regions of the East African mountains (one exceptional low record only from Mt. Kilimanjaro at 2500 m).

L. expansus is dioicous, but often fertile. It apparently lacks means of asexual reproduction.

43. Lophozia argentina (Steph.) Schust. (Jungermanniaceae) (Plate VII/40)

The species was known for a long time only on the basis of the type collection with uncertain locality (Argentina, coll. Lorentz); probably it is from the northern part of the country. Studying the African species of *Lophozia*, VÁŇA (1982) has found this species in the material collected by ESTERHUYSEN in Natal (Drakensberg) and erroneously recorded by S. ARNELL (1963), as *L. montaguensis* S. Arn. In Africa this species occurs "on cold wet rocky bank, S. aspect" at ca. 2500 m; as to the Argentinian locality ecological data are lacking.

Both populations are apparently dioicous and female (with perianths), but mature sporophytes were not yet seen.

44. Schistochila alata (Lehm.) Schiffn. (Schistochilaceae) (Plate VII/41)

Originally described from South Africa (leg. ECKLON), but more widely known from South America, where it occurs, according to ENGEL (1978) in Tierra del Fuego, the South Patagonian Channel region, on the Falkland Islands and, further north, on Juan Fernandez Is. (not on the adjacent Valdivian mainland). The species prefers wetter evergreen forests, where it is not uncommon at the base of large bryophyte mounds (ENGEL l.c.). Within the large, southern temperate — tropical montane genus (cf. SCHUSTER 1979) this is the only species with disjunct occurrence in America and Africa. A few species occur (partly *Paraschistochila*) in the tropical mountains of Africa, but, remarkably, the African distribution of *Schistochila* s.l. is restricted to the very old crystalline blocks and does not include the young volcanic mountains. In America no species penetrate into the tropical Andes. These facts coincide well with SCHUSTER's view (l.c.) on a very old, Gondwanalandic origin for *Paraschistochila* and *Schistochila* and even with the distribution of the above species, which is, most probably, uncapable to long range dispersal, its present distribution marking previous land connections.

All species are dioicous but spores are frequently produced, their size is of 17–23 μm in diameter. Gemmae are unknown in this species.

45. Tylimanthus limbatus Steph. (Acrobolbaceae) (Plate VII/42)

Syn.: *Marsupidium limbatum* (Steph.) Grolle; for further synonymy see ENGEL and GROLLE (1971).

This southern temperate Afro-American species (Tierra del Fuego to Northern Chile, Juan Fernández, S. Africa — see ENGEL and GROLLE l.c.) was recently discovered by JONES and PÓCS in the montane forests of Mt. Kilimanjaro (BIZOT and PÓCS 1974). Its disjunct occurrence on the geologically rather young Kilimanjaro volcano, where it grows in open, secondary *Myrica* forest, suggests arrival by long-range air dispersal. The possibility of a wider distribution of this species in East Africa, with occurrence for instance in the old block mountain range of Southeast Africa (intermediate between Mt. Kilimanjaro and South Africa) should not be ruled out.

The species is dioicous as all other representatives of the genus *Tylimanthus*, and may produce spores. About its mode of dispersal little remains known, however.

III.b. Wide southern temperate element, with penetration into tropical mountains and atlantic Europe

The seven species assigned to this group have a very interesting distribution pattern. They are more or less widespread in the southern temperate and subtropical zones and in the tropical montane belts of both continents, finally they irradiate to the atlantic islands, to Ireland and Britain or even to the western, oceanic part of continental Europe. Only two of them penetrate also into the atlantic, temperate coast of North America. It would be difficult to say, whether their present distribution (at least partly) reflects a Gondwanalandic origin and a European occurrence as the result of a later migration, or simply, a range to be explained by long range dispersal. All of them occur on the Macaronesian islands, which occurrence can be the relic of a former land bridge or even of a Tethyan distribution in the sense of Axelrod (1975); or these oceanic islands served, simply, as stepping stones in the way of the Gulf stream and air masses promoted by the sea current, which could carry diaspores from tropical America to atlantic Europe.

Anyway, based on their relationship, at least the two *Adelanthus* species, *Lepidozia cupressina* and *Telaranea nematodes* could have their origin on the former Gondwanaland, and taking in account the slow evolution in these groups, their dispersal could happen before its dissection. The two highly developed Lejeuneaceae taxa probably have another type of distributional history, in which long-range air dispersal might have played a much more important role.

46. Adelanthus decipiens (Hook. Mitt.) (Adelanthaceae)

This species, together with *A. lindenbergianus*, is discussed and mapped in detail by GROLLE (1969, 1972). Therefore we deal only briefly with them.

A. decipiens was not known until recently in the East African mountains, from where it was reported by BIZOT and PÓCS (1974, 1979) and by VÁŇA et al. (1979); it grows on Mt. Kahuzi, Kilimanjaro and in the Uluguru and Ukaguru Mts. at 2100–2900 m altitude, in the upper montane forest belt, as epiphyte or on rotten wood. It occurs also in the West African mountains, then in Transvaal and in South Africa (already at 660 m), on Tristan da Cunha and St. Helena. It does not occur in the southern temperate tip of the American continent, only in the tropical Andes from Bolivia to Venezuela, in Costa Rica, on the Galapagos Islands (800 m!) and on the Antilles. Finally it reaches Europe through the Azores, where it occurs in Ireland, Britain and Finistère in France.

It is dioicous and often produces spores, therefore SCHUSTER (1979) suggests the possibility of transatlantic air dispersal.

47. **Adelanthus lindenbergianus** (Lehm.) Mitt. (Adelanthaceae)

Its distribution pattern is very similar to the above species (see GROLLE 1969), but more southern in character. It is widespread in the temperate-subantarctic tip of South America, it occurs in the montane forests of the Andes and reaches Mexico as well (GROLLE 1972), but does not occur on the Antilles and in Macaronesia. It reaches Europe only in Ireland, but in Africa shows very similar distribution to that of *A. decipiens*, being widespread in the montane forests of East Africa and occurs in South Africa and in Lemuria but lacks in the West African mountains. It grows near the sea level (up to 700 m) in the temperate regions, while ascends up to 2100 m in the subtropics and up to 3900 m in the equatorial mountains. In the tropics it lives on bark, on shady rocks or on rotting logs of montane forests.

Dioicous species, producing 12–16 μm large spores. Vegetative reproduction is also known by gemmae, developing quite rarely on the apical part of the leaf margin. As the European populations are sterile, SCHUSTER (1979) suggests a recent arrival there via air transport of gemmae.

48. **Colura calyptrifolia** (Hook.) Dum. ssp. **calyptrifolia** (Lejeuneaceae) (Plate VIII/43)

Although VANDEN BERGHEN (1972*a*) stated, that *Colura tenuicornis* Evans differs only in quantitative characters from *C. calyptryfolia* and treated the two taxa, as subspecies of the latter, typical *C. calyptrifolia* has a very distinct distribution pattern (see also JOVET-AST 1954: 13–14). While *C. tenuicornis* (or *C. calyptrifolia* ssp. *tenuicornis*) is clearly pantropical in distribution, *C. calyptrifolia* is an oceanic-temperate Afro-American (+ European) species.

In addition to the knowledge about its distribution presented in the monograph of the genus by JOVET-AST (1953, 1954), *C. calyptrifolia* s. str. has become known also from Africa, from the tropical montane forests of Transvaal (ARNELL 1963: 178) and Tanzania (West Usambara Mts., PÓCS ined.), and from the surrounding islands, as Tristan da Cunha (ARNELL 1958: 7) and from Mauritius (JONES 1979: 388).

Colura calyptrifolia is either epiphyllous or grows more often on twigs and bark of mostly ericaceous shrubs, in the tropical mountains between 1000 and 2000 m, while in oceanic-temperate areas near the sea level.

The plant is monoicous and produces large (40–65 × 20–30 μm) spores and also abundant discoid gemmae.

49. **Lepidozia cupressina** (Sw.) Lindenb. (Lepidoziaceae) (Plate VIII/44)

If we treat the species in broad sense (PÓCS 1984), by combining the many overlappings and transitional forms between related taxa treated separately many times, it has a tricentric distribution pattern. In America it is widespread from the southern subantarctic and temperate zones through the Andes to the Caribbean region. In Africa it is known from subtropical Cape through Natal and Transvaal to the mountains of East Africa, finally from the Mascarenes to atlantic Europe including a small part of Norway with very oceanic climate. The most primitive forms are known at the temperate parts of South America and in South Africa, while in the Andes and East African mountains and in atlantic Europe a secondary evolution took place at subspecies level, which well reflects a Gondwanalandic origin.

In the tropical mountains *L. cupressina* occurs on the acid ground and on the bark of trees of montane evergreen forests between 1000 and 3000 m altitude, sometimes penetrating in the tropic alpine vegetation up to 3600 m. On the other hand, it descends near to sea level in the temperate zones.

Lepidozia cupressina is dioicous and reproduces by spores, but sporophytes do not develop too often. Asexual mean of propagation is not known.

50. Leptoscyphus cuneifolius (Hook.) Mitt. (Geocalycaceae)

The taxonomy and distribution of this species are thoroughly discussed by Grolle (1962), accompanied by a map. More recent records are enumerated by Schuster (1980: 278). The species is more or less bipolar in distribution. In the northern hemisphere it occurs on both sides of the Atlantic Ocean; in the Appalachians of eastern USA, in the Azores, Madeira, Ireland and Great Britain and SE Norway. It penetrates in the tropical region in the Caribbean, where it becomes an inhabitant of montane evergreen forests, as in Cuba (Váňa ined.), Jamaica, Dominica, Mt. Roraima in Guyana and in the Venezuelan and Colombian Andes, where it grows between 3000 and 3500 m (Gradstein and Hekking 1979). In the southern hemisphere it occurs quite isolated from the northern population, being widespread from Juan Fernandez Is. to the Magellan Strait and in Tristan da Cunha. In his monograph of *Leptoscyphus* Grolle (l.c.) distinguished the southern population as ssp. *fragilis* (Jack et Steph.) Grolle, but later synonymized it with the typical subspecies, which was confirmed by Schuster (l.c.). It is remarkable, that the species does not reach the eastern world sector in continental Africa (only Atlantic islands and Europe), although, being such a delicate plant, it could easily have been overlooked in African material.

In the Southern Appalachian Mts. it grows in fog forests on the bark of *Abies fraseri* (Schuster l.c.), while in Cuba lives in montane evergreen mist forests (fangales, monte nublado) on bark of trees, at 1100 m altitude (Pócs ined.). On other Caribbean islands and in Colombia it is known as a ramicolous species in the mossy forests and shrubs of higher mountains, while in Chile it occurs on the bark of *Nothofagus* trees (Schuster 1980: 279). On the Azores, according to Sjögren (1978) it is known as epiphyte or epilithic, usually growing intermixed in dense moss carpets of *Juniperus brevifolia* forests. The above habitats and the oceanic distribution of the species reflect its high demand on atmospheric humidity.

Dioicous species, rarely producing spores, but asexual mean of reproduction by caducous leaves and underleaves is always present.

51. Lejeunea (Microlejeunea) ulicina (Tayl.) Tayl. complex (Lejeuneaceae) (Plate VIII/45)

It depends on the species concept used, whether we treat this complex, as members of a subtropical-tropical vicariant species pair or as two subspecies of a northern temperate species, *Lejeunea ulicina.* As Schuster dealt in details with the delimination of the taxa belonging here (Schuster 1962, 1979: 1067), involving statistics made on many specimens belonging to this complex. We accept his concept, treating the taxa concerned as subspecies. This case there are three subspecies at hand;

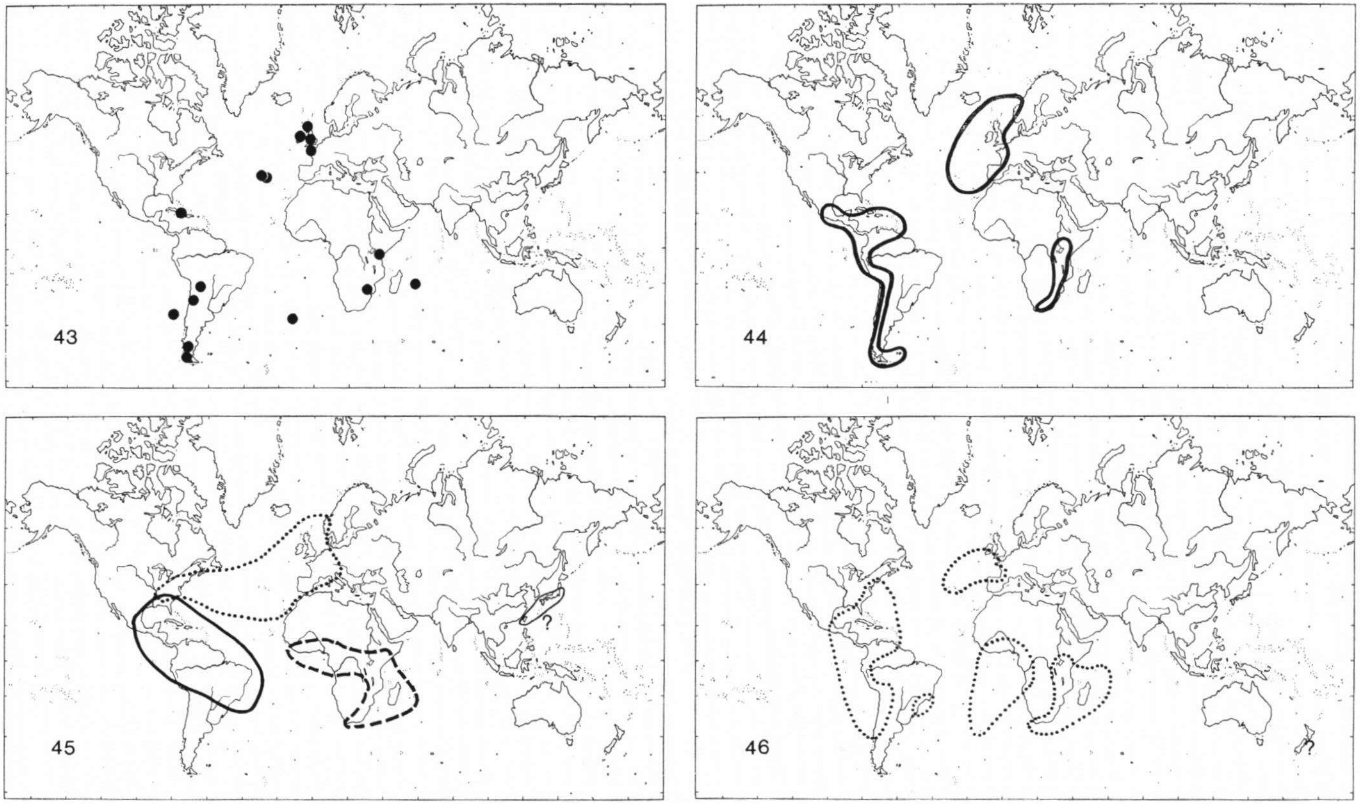

Plate VIII

Southern temperate species in wide sense, penetrating into atlantic Europe. 43. *Colura calyptrifolia* (Hook.) Dum. 44. *Lepidozia cupressina* (Sw.) Lindenb. 45. *Lejeunea* (*Microlejeunea*) *ulicina* (Tayl.) Tayl. ssp. *ulicina* (dotted line), ssp. *bullata* (Tayl.) Schust. (solid line) and ssp. *ocellifera* (S. Arnell) Schust. (broken line). (Thin line marks Japanese populations of *L. punctiformis* Tayl. assigned to *L. ulicina* ssp. *ulicina* by Schuster and Inoue.) 46. *Telaranea nematodes* (Gott. ex Aust.) Howe. ?: *T. herzogii* (Hodgs.) Hodgs. with obscure relation to *T. nematodes*

a) *Lejeunea ulicina* (Tayl.) Tayl. ex G., L. et N. ssp. *ulicina*

Distributed on both sides of the Atlantic Ocean, in the areas affected by oceanic climate and growing on rocks and bark, on rotting wood or rarely on living bryophytes, in dense (mostly deciduous) forests up to 1800 m altitude. According to SCHUSTER (l.c.) some Japanese populations assigned to *L. punctiformis* are also referable to this ssp. INOUE in his recent paper (1981) seems to accept and even extend the presence of *L. ulicina* in Japan and to the whole area formerly known as of *L. punctiformis* in Southeast Asia.

b) ssp. *bullata* (Tayl.) Schust.

Syn.; *Lejeunea bullata* Tayl.
Microlejeunea bullata Evs.
(See further synonymy in SCHUSTER 1980: 1074)

Its area just overlaps that of the first subspecies in the southeastern United States and it is widespread in the Caribbean region and the northern half of South America. It occurs both as corticolous and epiphyllous, rarely also on rocks or on ground, up to 3000 m in tropical America (BISCHLER et al. 1963).

c) ssp. *ocellifera* (S. Arnell) Schust.

Syn.: *Microlejeunea africana* Steph.
Microlejeunea ocellifera S. Arnell

Very common and widespread in the wetter parts of tropical and South Africa, where it occurs from the sea level up to 2100 m in the lowland and montane forests belts, first of all, as epiphyllous and corticolous species. According to JONES (1969) it occurs in the lowland rain forests of West Africa, where it is very common, usually on the bark of tree boles and branches.

All subspecies are dioicous (if *L. punctiformis* separately exists) and often produce perianths, while the sporophytes are unknown. As no kinds of asexual propagation are at hand, it remains obscure, how the species can be such a successful pioneer on shady, wet bark or living leaves, not mentioning the very large area of distribution. One must think about vegetative propagation by fragmentation and easy survival of the detached plant fragments.

52. **Telaranea nematodes** (Gott. ex Aust.) Howe (Lepidoziaceae) (Plate VIII/46)

T. nematodes has a distribution pattern very similar to that of the previous 6 species, but conspicuous by its penetration into the temperate region of USA as north as to New York (SCHUSTER 1969). Following the atlantic coast line, it becomes very widespread in the Caribbean region, in the tropical Andes and occurs again in the south Brazilian highlands. In Africa it is bicentric, occurring in the Guinea-Congo rain forest basin and South-East Africa including Madagascar and the Mascarene islands. It should be checked, whether *Telaranea herzogii* (Hodgs.) Hodgs. in New Zealand is only closely related or conspecific with it. *T. nematodes* occurs in Europe only along the warm-temperate, oceanic coast.

In the wettest tropics, like in the upper Amazonas or Congo basin, it occurs even near the sea level, growing together with *Arachniopsis diacantha*, which is similar in appearance. It is quite common in tropical montane forests up to about 2000 m altitude and penetrates even in the páramo vegetation belt (up to 4250 m in Colombia !, GRADSTEIN and HEKKING 1979). It grows usually on acid ground, rotten wood or on litter, on peaty soil of bogs, rarely on rock surface, usually associated with other Lepidoziaceae species.

It is dioicous and often produces spores (14–17 μm in diameter). Asexual reproduction is not known.

Discussion

Taxonomic relations

The greatest part of disjunct, bicontinental lowland tropical taxa belongs to the family of Lejeuneaceae, while other patterns are found in other, mainly Jungermannialean groups, from throughout various families except *Plagiochila*. This may illustrate the high level of regional speciation within this giant genus undergoing present evolution.

Among thallose liverworts there are only very few examples (*Aneura pseudopinguis*, *Metzgeria albinea* still incompletely known and not discussed), but significantly the subtropical disjuncts are exclusively thallose (*Exormotheca*, *Sphaerocarpos*), which relates to the dominance of thallose taxa in these areas. A large genus, in which macro-disjuncts are rare (like in *Plagiochila*) may be *Riccardia* (no evidence found thus far, fide JAN MEENKS who checked material from both continents).

The above conclusions also hold for the Afro-Asiatic and pantropical taxa (see lists in BIZOT and PÓCS 1974, PÓCS 1976 and unpublished records). The total number of macrodisjunct tropical liverwort species known is now about 95 in Africa (40 Afro-Asian; 35 Afro-American; 20 pantropical).

Ranges

The maps show continuous or discontinuous distribution patterns on each continent. Continuous distribution is seen mostly in case of tropical lowland species, like *Acrolejeunea emergens*, *Radula flaccida*. Discontinuous areas are much more common, the reasons are:

1. *Ecological barriers:* in the case of most montane and alpine elements or, even, by lowland rain forest elements occurring in a generally drier environment with isolated forest patches, like in case of *Pycnolejeunea contigua* in East Africa. The montane taxa are potentially quadricentric: Andes with the West Indies, SE Brasil; West Africa (local), finally East and South Africa with the Lemurian islands. *Radula boryana* and *Symphyogyna brasiliensis* have almost "complete quadricentric" ranges, while others miss from one or two of these centres. Reason may be insufficient exploring (see below). The alpine taxa are usually bicentric: Andes and East African high mountains (*Andrewsianthus jamesonii* or *Gymnocoleopsis multiflora*). When their altitudinal range extends to the montane belt as well, their distribution becomes larger (e.g. *Herbertus subdentatus*). *Isotachis aubertii* is unexpectedly lacking from the Andes and the reason may be also insufficient exploration.

2. *Insufficient exploring*: ranges for the tiny and possibly overlooked *Aphanolejeunea exigua*; the crown epiphyte *Lejeunea unciloba*; species growing in habitats often ignored by non-specialist, like shaded banks (*Andrewsianthus*

jamesonii) or species visible in dry areas only during the rainy season not favoured by visiting botanists.

3. *Insufficient taxonomic knowledge*: although the fragmentary range *Lejeunea autoica* is explanable by a possible polytopic evolution, it is much more reasonable, that this species is still hidden among the many unrevised materials belonging to the taxonomically difficult genus *Lejeunea*. This may be the reason also for the very fragmentary knowledge about the American distribution of *Aneura pseudopinguis* and some other taxa.

4. *Relict distribution relating to Gondwanic origin:* potential habitats for such genera, as *Bryopteris* and *Symbiezidium* are plentiful on the African mainland, yet lacking there. The very restricted ranges of *Arachniopsis* dissotricha and the vicariant *A. diplopoda* are to be explained also by their relict character. The case of "peri-Afro-american element" was discussed in detail for *Symbiezidium*, on page 140 as the case of species restricted to geologically old mountains, not being capable to long-range dispersal, as well (PÓCS 1982, VAN ZANTEN and PÓCS 1981, and by *Schistochila alata* on page 157 of this paper).

5. *Unknown reasons*: for example in the case of *Stephaniella paraphyllina*, which is widespread in the Andean region, it is obscure, why it does occur only at a single place in Africa, where similar environmental conditions are assured at many places. The African locality could be explained by one single successful case of long-range air dispersal but also by the relict character of a former wider distribution in Africa. There are no indications that the species might have been introduced by man, as in the case of the Mexican locality of *Exormotheca pustulosa*.

Dispersibility

The ability for long-range or short-range air dispersal, or step by step land dispersal is the main factor, which can influence the range of species and is responsible for disjunct distribution along the dissection of land masses and along other geological and climatic changes. The dispersibility of species depends upon several factors (see also Introduction):

1. *Sexuality*: almost all disjunct Lejeuneaceae are autoicous. Within *Acrolejeunea* the widespread spp. are autoicous, local spp. normally dioicous (GRADSTEIN 1975). The single dioic species among Afro-American tropical lowland element is *Radula flaccida*, which has copious gemmae.

Contrasting with tropical lowland species, montane, alpine and other spp. are mainly dioicous, although some may develop gemmae (*Andrewsianthus jamesonii*). It seems that the dioicous condition is more common in temperate species. Yet, in all spp. sporophytes occur, so long-range dispersal via unisexual spores may still be possible, although the chances for successful establishment are lower. It can be concluded, that sexuality is not evidently reduced in the macro-disjunct species contrary to local, endemic liverworts.

2. *Asexual reproduction and dispersal by fragmentation*: on the whole, only few spp. (ca 25%) have special asexual means of reproduction (gemmae, cladulae). Fragmentation might be very important in the alpine species (*Stephaniella*, *Marsupella*), which often grow on loose, dry, bare ground of open plant communities. There are observations on byrophyte fragments successfully germinated after melting from arctic icefields, which seems to prove the survival ability of liverwort fragments under dry and low temperature conditions.

3. *The resistance of diaspores*: as VAN ZANTEN and PÓCS (1981) discussed in details, we know much about the drought and cold resistance of moss spores, but much less about that of the liverworts. According to FULFORD (1951) protonematal spores of Lejeuneaceae are little resistant and not suitable for long-range dispersal. However, this has not been tested, although she experienced, that even one hour exposure under laboratory air conditions killed the spores of Lejeuneaceae, *Lepidozia* and *Ptilidium*.

4. *Spore size*: as mentioned in the Introduction, diaspores must be small enough for aerial transport. Checking our Afro-American liverwort species from this point of view (not the vicariant species pairs and Afro-American genera), only 14 species fall in the category of sizes apt for easy long-range air transport, the spore size in eight species being definitely much larger than 25 μm and in 15 species unknown. Asexual gemmae are also to be tested from this point of view.

5. *Suitable habitat and competing ability*: from this point of view "weedy" species occurring often on bare surfaces, as recent lava rocks, roadcuts or, as epiphytes, in secondary habitats (isolated palms and orchard trees, plantations, forest openings) are such, which one should expect to have arrived by long-range air transport and aggressive enough to compete with other species. To a large extent, "weedyness" often correlates with commonness (cf. GRADSTEIN and WEBER 1982: 134) and many species among the disjuncts fall in this category being at least locally weedy: *Acrolejeunea emergens*, *Cololejeunea cardiocarpa*, *Herbertus subdentatus*, *Isotachis aubertii*, *Lophocolea martiana*, *Schiffneriolejeunea polycarpa*, *Symphyogyna brasiliensis*, etc. On the other hand, many common, "weedy" species are not bicentric disjunct and apparently restricted to one continent only, as the American *Dicranolejeunea axillaris*, *Frullania brasiliensis*, *Leptolejeunea elliptica*, *Leptoscyphus porphyrius* or *Plagiochila guilleminiana* and the African *Cololejeunea pusilla*, *Frullania caffraria*, *Marchantia parviloba* or *Plagiochila terebrans*. These may be "chance endemics" in the sense of ZANTEN (1978: 471), if their diaspores are apt for long-range air dispersal.

The occurrence of such species on isolated, ± young oceanic islands seems to confirm their air dispersal. From the discussed Afro-American species *Symphyogyna brasiliensis* (Ascension, Tristan da Cunha), *Syzygiella concreta* (Tristan), *Isotachis aubertii* (Ascension), *Exormotheca pustulosa* (St. Helena), *Leptoscyphus expansus* (Tristan), *Hyalolepidozia bicuspidata* (Tristan), the two *Adelanthus* (Tristan), *Colura calyptrifolia* and *Telaranea nematodes* (Tristan) and some others occur on the islands along the Atlantic ridge. Most of these are weedy on the mainland, hence aggressive which should have helped their dispersal on the not too old volcanic islands.

Final conclusion

Most Afro-American species seem to be common in parts of their ranges and thus well capable to step by step dispersal. Even though in some spp. we find few indications of copious diaspore production, an occasional or isolated case of long-range air dispersal could well be assumed as having caused the

Table 3

A listing of further supposed tropical Afro-American vicariant species pairs, partly of unverified taxonomic status

American taxa	African taxa
Archilejeunea spp.	*Archilejeunea africana* Steph. and allies
Brachiolejeunea chinantlana (Gott.) Schiffn.	*Brachiolejeunea tristis* Steph.
Calypogeia peruviana Nees et Mont.	*Calypogeia afrocoerulea* E. W. Jones
Calypogeia cellulosa (Spreng.) Steph.	*Calypogeia fusca* (Lehm.) Steph.
Caudalejeunea lehmanniana (Gott.) Evans	*Caudalejeunea hanningtonii* (Mitt.) Schiffn. and allies
Cololejeunea bischlerana Tixier	*Cololejeunea hyalino-marginata* (Nees et Mont.) Grolle
Cylindrocolea rhizantha (Mont.) Schust.	*Cylindrocolea atroviridis* (Sim) Váňa
Drepanolejeunea bidens Steph.	*Drepanolejeunea cultrella* (Mitt.) Steph.
Frullania riojaneirensis (Raddi) Ångstr.	*Frullania africana* Steph.
Lophocolea trapezoidea Mont.	*Lophocolea muhavurensis* (S. Arn.) S. Arn.
Marchesinia brachiata (Sw.) Schiffn.	*Marchesinia excavata* (Mitt.) Steph. and allies
Marsupella trollii Herz.	*Marsupella capensis* S. Arn.
Odontolejeunea lunulata (Web.) Schiffn.	*Odontolejeunea tortuosa* (L. et L.) Steph.
Pallavicinia erythropus (Gott.) Steph.	*Pallavicinia spinosa* (L. et L.) Grolle
Plagiochila columbica Gott.	*Plagiochila integerrima* Steph.
Porella swartziana (Web.) Trev.	*Porella capensis* (Gott.) Steph.
Rectolejeunea pililoba (Spr.) Schust.	*Rectolejeunea setacea* (Steph.) Schust.

macro-disjunction. In some other cases production of diaspores apt for long-range air dispersal is apparently lacking. It is hard to visualize that evolution went so slow in these "successful" species, that they did not evolve since the breaking up of western Gondwanaland. However, this could have caused very well the disjunction of genera, the vicariant species pairs in many cases and in some, exceptional cases the disjunction of species in archaic groups, where evolution remained slow. Fossil finds in amber (GROLLE 1981) confirm that eocenic species belong to still existing genera and that "Ginkyo-type" relict occurrences may be present even in "advanced" groups of liverworts, as *Nipponolejeunea* (Japan; fossil also in Europe).

A correlation with level of evolutionary advancement, as SCHUSTER (1969) postulates for the southern temperate regions, needs more taxonomic and floristic data than currently available for the tropics, hence results in too much unfounded speculation. Also, it needs to focus on all types of ranges (including the endemic), not just the macro-disjuncts.

Further research should involve taxonomic work on supposed vicariant species pairs (e.g. Table 3), strenghtening the arguments and explanations when more examples appear. Also, we have to know much more about the resistance and dispersal ability of Hepatic diaspores, proved by experiments. Of course, any increase of the meagre paleontological evidence might help in the understanding of liverwort dispersal in relation to their evolution and to the geological events.

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