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Manual of Tropical Bryology

by

Jan-Peter Frahm

with contributions by

BRIAN O'SHEA, TAMAS POCS, TIMO KOPONEN, SINIKKA PIIPPO, JOHANNES ENROTH,
PENGCHENG RAO & YIN-MING FANG

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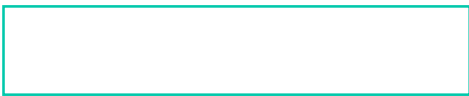
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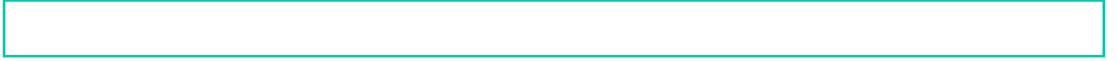
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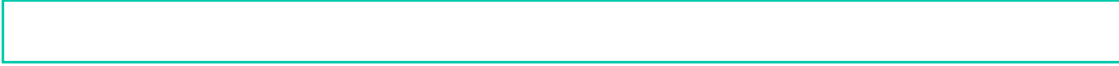
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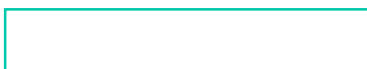


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Preface

It is still a fact that most bryologists per area are found in the temperate regions of the northern hemisphere, who have spent up to 200 years (as in Europe) in the exploration of their bryofloras with the result that these countries have not only floras for identification of the comparably low number of species but some countries have already detailed grid maps of the distribution of all species. On the other hand, there are vast regions in the tropics which are very insufficiently explored. So far, the knowledge of bryophytes in these regions was predominantly provided by scientists from North America, Europe or Japan. Still much work is done by scientists and - during the past decades also increasingly - even by advanced amateurs from these countries. Regretably, these activities are often misunderstood by local biologists in the tropics and especially by the authorities of these states as scientific exploitation, and recently collecting of material for genetic studies as plundering of genetic resources, which is nonsense but makes research difficult or even impossible in such countries. In this regard, the question raises why there are so few bryologists in tropical countries and even no bryologists in many countries? Usually, the lack of resources such as laboratories, money, libraries, herbaria etc. is presented as arguments, which does not match the point, since many bryologists in industrial countries suffer from similar restrictions and sometimes have worse working conditions than colleagues in tropical countries, but make nevertheless valuable contributions to tropical bryology. Even amateurs have contributed a lot to tropical bryology in the past. The fewest bryologists work in such famous places as Missouri or New York Botanical Garden. Many of them are from eastern, former communistic countries and never gave up to promote tropical bryology under these conditions. In my opinion, the most crucial point is that students in tropical countries get not in contact with bryophytes, and mainly because of the lack of literature. Nobody can expect that students pick up a subject for their thesis if there is no literature available. This manual is therefore devoted to these students. Possibilities to gain a bryological training in industrial countries and paid by these countries were used only by few students, although available. And if these students do not come to us, we have to go to them (which is even cheaper). This is the reason for the increased number of courses on tropical bryology in the past.

Another group of potential users of this manual are bryologists, especially amateur bryologists from industrial countries. The bryological exploration in these countries has made such progress during the last 200 years that these countries are comparably good explored. Recent activities concern the distinction of "small species" or mapping. Some countries e.g. Great Britain are even "ready mapped". Therefore the bryological activities are directed towards tropical countries. Checklists can even be compiled without leaving the desk. In the 19. century, collections in tropical countries were usually performed during scientific expeditions financed and operated by governments of colonial states, rarely by individuals, adventurers, who gained their lives by selling their collections. Later, scientific institutions organized trips to the tropics to enhance their collections. Today, relatively cheap air fares allow amateurs from industrial countries to spend their holidays in the tropics and to make new discoveries, which they cannot make at home. By this way, some amateurs have made most valuable contributions to the floristic knowledge of tropical countries, and by this way the members of the British Bryological Society Tropical Bryology Working Group are more numerous than all bryologists in Africa or SE-Asia. The activities within the society have led to the preparation of checklists, detection of numerous new records and even new species in Malawi and Uganda. Local botanists in the tropics should appreciate this and not interpret it as new scientific imperialism. It brings us small steps forward towards an understanding of tropical bryology. Regretably, bryological activities of "tourists" were more numerous in some tropical countries than those of native full time bryologists. Paradoxically, activities of bryologists from non-tropical countries in the tropics were and are generally

still much larger than those of local bryologists. The activities of amateurs contradict also the argument that bryological research in the tropics is not possible without large libraries, herbaria, lab space, or personel. Even lacking budgets are no arguments: the German Research Foundation paid hardly more for projects in the tropics than flights (which local botanists do not need) and a car rental (which local botanists do not need because of an own car). And the professors stay in tents and cook on kerosine stoves, something which many local botanists from tropical countries would not do. Therefore this small manual may also stimulate bryologists from extratropical countries to focus their interest in tropical bryology.

A short previous version of this manual was originally written by the author as script for the „curso taller sobre briofitos tropicales“ held at the Jardín Botánico de Mérida, Venezuela, Feb. 24. - March 7. 1997 together with Tamas Pócs. It covered some topics of the course in a textfile, which was distributed on disk, but was not complete. The printout as well as the disk version did not include illustrations (which were presented during the course as slides). Furthermore, this script was focussed on the neotropics.

Aim of this course and this script was to provide some knowledge of tropical bryology. It required, however, a basic knowledge of bryology, for which textbooks shall be consulted. Therefore general topics such as life cycle, anatomy, morphology, and systematics are omitted here.

More courses on Tropical Bryology have been held for European postgraduate students in 1993, 1998 and 2000 in the Division of Systematic Biology, University of Helsinki, organized by Timo Koponen and Johannes Enroth, made possible by funds of the European Community. Due to the lack of alternatives, this Mérida-script was used as compendium for the courses in 1998 and 2000. For that purpose, Timo Koponen and Johannes Enroth added illustrations and did some editorial work. It was, however, still a fragment. Some efforts were later undertaken to get some colleagues interested to complete this course script to a short manual, but in vain. Therefore I started to complete this script myself with the consciousness that a joined work of several specialists would have been better. I know that some colleagues argue that such a booklet should have better not written since it is not complete or contains errors. The latter is true, but in my opinion the lack of such a small compendium is even worth. But only those who do nothing make also no mistakes except for the mistake to do nothing. It is therefore hoped that this small volume of „TROPICAL BRYOLOGY“ will raise interest in this much neglected group of plants, increase bryological activities in the tropics and stimulate to include bryophytes in studies of biodiversity and ecology of tropical forests.

This manual has some limitations: because of copyright problems, the illustrations are mostly taken from own publications or from the journal *Tropical Bryology*. Redrawing existing illustrations would have been too time consuming. Next, the explanations are mostly based on tropical rain forest bryology. Other habitats are covered only to an lesser extend. Reason is simply that bryological research in the tropics is focussed on rain forests, which harbours most of the tropical bryophytes. This will not say that other bryological aspects in the tropics are not as interesting. And finally, the explanations are not complete in some respects, it is not a complete textbook but still an extended course script, but anyway, this manual will now be available not only for course participants but a wider range of interested bryologists especially in the tropics, and - as mentioned before - better than nothing.

This volume is, like all volumes of „TROPICAL BRYOLOGY“ available as faksimile edition on CD-ROM as pdf-file, which allows to print all or parts of it or to copy and paste parts of the text e.g. references into other applications.

I wish to thank Brian O'Shea and Tamas Pócs, who contributed parts to this volume, as well as Timo Koponen, Sinikka Piippo, Johannes Enroth, Pengcheng Rao and Yin-Ming Fang, who had completed earlier versions of the course script.

Bonn, April 2003

Jan-Peter Frahm

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1. INTRODUCTION

Bryophytes belong to the oldest land plants. They existed already in the Palaeozoic 300 mio years ago in forms which were hardly different from the extant species. They remained relatively unchanged with relatively low evolution rates (and are thus often called a „conservative“ plant group), but could successfully establish themselves in an always varying environment from Devonian swamps to Permian forests, Mesozoic deserts and as epiphytes in Tertiary rainforests. They are not eaten by snails or insects, and are resistant against fungi and bacteria.

Whereas the species numbers of lycopods and horsetails have decreased over the past geological periods, bryophytes seem not to have been decreasing but have perhaps even increased their diversity by occupying new ecological niches, such as epiphytic existence in forests.

Bryophytes are so called „lower plants“ which, however, does not mean that they have primitive morphological structures. The presence of stomata, conducting tissues and a cuticula in many species (structures which are, interestingly, no more functional), shows that bryophytes had the ability to develop cormophytic structures, but instead they chose a poicilohydric existence as an alternative to a cormophytic one.

Bryophytes grow in an astonishingly broad variety of substrates and habitats. They occur in the snow vegetation with a 9 months' snow cover, form masses in the tundra and in the boreal forests, cover tree trunks in tropical rain forests, grow 50 m deep in lakes and at 5000 m altitude on mountain peaks, in extremely acid peat bogs,

and on heavy metal rich soil, in canopies and deserts, in dark caves and on exposed rocks. This is rendered possible by various morphological, anatomical and physiological adaptations. Thus bryophytes are not at all „primitive“ plants.

Bryophytes are a much neglected but nevertheless an important group of plants:

1. They are the second largest group of green land plants (with ca. 15000 species).
2. They play an important role in many ecosystems such as tundras, bogs and tropical rainforests (the extension of bogs in the boreal zone is much larger than that of the tropical rain forest, although this zone appears relatively small in certain map projections). In these ecosystems, bryophytes play an important role in
 - water storage
 - nutrient uptake from rain
 - ecological interactions (habitat for animals).
3. Because of their sensitivity to water loss, bryophytes are good indicators of
 - microclimate
 - altitudinal zonation of rain forests.
4. This makes bryophytes useful also in biodiversity research.
5. Bryophytes absorb water and nutrients exclusively or mostly by their surface and do not filter water and nutrients through soil and roots as flowering plants. They are therefore good indicators of
 - pollution of air and water
 - heavy metal contamination
 - radioactivity.
6. Due to direct reaction to climatic factors and short life cycles and spore dispersal, bryophytes

are also good and very fast indicators of climatic changes.

Bryophytes of tropical rain forests have several advantages as compared with flowering plants:

- They are much less numerous than flowering plants. There are about 250.000 species of flowering plants in the world as compared with 10-15.000 species of bryophytes. There are no more than 5000 species of bryophytes in the neotropics, presumably even less. In Colombia there are about 1000 species of mosses as compared with 45-55.000 species of flowering plants. Thus a wide knowledge of a regional mossflora can be obtained relatively soon, but never for flowering plants.

- Bryophytes have much larger geographic ranges than flowering plants. A major part of the species in different parts of the neotropics are identical. The neotropic element accounts for about 40% of the species. Many Andine species range from southern Mexico to northern Argentina. Thus bryologists can work in different parts of the tropics with the same results. Nevertheless there are also endemic bryophyte species indicating local phytogeographical characteristics. Also comparisons of species diversity of distant areas is possible by the small ranges.

- The density of bryophytes is much higher than in flowering plants. Studying a hectare results in representative data for the whole altitudinal zone.

- Sterile plants can usually be identified whereas flowering plants need mostly to be in flower for identification.

Nevertheless, the knowledge of tropical bryophytes is still very poor. There are only few bryologists in the tropics. In Latin America, at present only about 25 in Mexico, Costa Rica, Panama, Puerto Rico, Colombia, Venezuela, Brazil and Argentina. The situation in tropical Africa is much worse with few bryologists only in Nigeria, Kenya, Uganda and Malawi.

However, studying tropical bryophytes is very important because:

- Floristic surveys will probably not result in the detection of many undescribed species as in other groups of organisms (e.g. insects), but will result in the knowledge of biodiversity (e.g. „hot spots“, centers of biodiversity); will give valuable information for nature conservation; will result

in the knowledge of geographic ranges, which reflect evolution and vegetation history.

- Study of phytochemical compounds of bryophytes will give knowledge of chemical compounds with anti-microbial and anti-tumor effects. Natural compounds will replace artificial substances e.g. as biocides.

- Knowledge of tropical species will enhance our knowledge of the systematics, since the majority of species occurs in the tropics.

- Study of the anatomy of tropical species has brought extremely interesting results, e.g. the presence of vessel-like canals in the stems of *Hypopterygium*.

- Knowledge of the ecology of bryophytes, especially of the epiphytic rainforest bryophytes, will enhance our knowledge of the importance of bryophytes in the ecosystem.

Bryological activities in the industrialized countries are going rapidly down due to a shortage of positions. The activities at universities are today focused on molecular biology and, consequently, classical bryological positions are no more held and taxonomic or phytogeographic studies can not even survive in botanical museums. Therefore bryology must be established in tropical countries „in situ“. The partial aim of this volume is therefore to develop in the students an interest in bryology, to stimulate studies and to facilitate bryology in tropical countries.

General literature

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Guide to bryofloras in the world:

Greene, S.W. & Harrington, A.J. 1989. The *Conspectus of Bryological Taxonomic Literature. Part 2. Guide to national and regional literature. Bryophytorum Bibliotheca 37.*

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British Bryological Society, Tropical Bryology Working Group with activities in Malawi and Uganda, see www.rbge.org.uk/bbs/bbs.htm.

Funding

Sastre, I., Tan, B.C. 1995. Directory of grants and scholarships for bryologists. *Bryol. Times* 83/84: 1-4.

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Textbooks

Delgadillo M., C., Cárdenas S., A. (1990). *Manual de Briófitas*. 134 pp., Mexico-City.

This highly recommended book for Latin American students provides a basic knowledge of bryology (life cycle, morphology, physiology, ecology, phytogeography, cytology, evolution and commercial use. It includes in addition some proposals for practicals and a key and description of common bryophyte genera in Mexico.

Frahm, J.-P. 2001. *Biologie der Moose*. Heidelberg (Spektrum). (in German, Spanish translation in preparation).

Shaw, A.J., Goffinet, B. 2000. *Bryophyte Biology*. Cambridge (Cambridge University Press).

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2. DIVERSITY OF BRYOPHYTE SPECIES IN THE TROPICS

2.1. Global diversity

The actual number of bryophyte species is given in classical botanical textbooks as 25.000 (15.000 mosses, 10.000 hepatics), a number probably going back on a count of the species included in the volumes of Engler-Prantl's „Natürliche Pflanzenfamilien“ at the beginning of the 20th century. About 57.000 species of mosses have been described in total (Crosby et al. 1992). Their names are listed in the „Index Muscorum (Wijk et al. 1959-69), which includes all names published until 1963. The additions from 1963-1989 are included in the „Index of Mosses“ (Crosby et al. 1992), those from 1990-92 in a supplement (Crosby & Magill 1994). Walther (1983) has counted all legitimate moss species in the „Index Muscorum“ and Supplements to 1977 and came up with 16.455 species. On the other hand, critical revisions of genera result in a considerable „loss“ of species. According to Touw (1974), the percentage of recognized taxa in revisions and monographs varies between 20 and 40% of the original number. Of the taxa described since 1930, 73% have been reduced to synonymy. Examples of reduction rates in taxonomic revisions are indicated in the taxonomy-chapter. Crosby et al. (1992) estimate that there are 10.000 species of mosses. There are no actual approximations of numbers of hepatics in the world, which can be estimated with about 4000. It has to be kept in mind that mosses and hepatics (with hornworts) have very different diversities. Mosses are much more drought tolerant than hepatics (with a few exceptions of Marchantiidae). Therefore hepatics can be used as indicators for humid climates. Even in North America and Europe, we have a decrease of hepatics from the oceanic west coasts to the interior of the continents with decreasing

precipitation and humidity, but again in increase in the mountains. The same counts for the tropics. Therefore the ratio hepatics : mosses can be successfully and easily used to characterize different climatic conditions of relevées in different altitudes or distance to the ocean. The bryoflora in the tropics may consists of 40% hepatics in some regions but this percentage may increase to 90% in hyperhumid regions such as the Chocó region in Colombia, which is one of the places in the world with the highest precipitation.

Two thirds of all bryophyte species or about 8000 species occur in the tropics. This is the reason that tropical bryology needs to be focussed. In contrast, there are about 1600 species of bryophytes in Europe, which are covered in 32 floras (1:50). In contrast, the 8000 bryophyte species in the tropics are covered by 16 floras (1:6000). With regard to the humid tropics, the percentage of liverworts and hornworts is much higher than in other regions of the world.

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2.2. Regional diversity

Regional diversity depends on

- the climate of the area
- the geological age and history of the area, especial plate tectonics
- the availability of species
- high diversity of habitats.

Size is not an important factor, since small regions can have much more species than large regions. Regions with high diversity (so called „hot spots“) are characterised by a high diversity of habitats, a long geological history without dramatic changes (arid periods, glaciation periods), a favourable climate and a rich source of native species or immigrants and factors stimulating the evolution (raise of mountains, isolation on islands).

Diversity is expressed by species numbers per area. On a global scale, a worldwide used unit is 10.000 km², however, diversity is also counted on smaller units down to a hectare or a tree.

Diversity in a place is composed

- from the original stock of species
- by immigrants (e.g. through the chain of the Andes, by mountain hopping in tropical Africa or island hopping in tropical SE-Asia
- by secondary evolution.

Thus the diversity depends also on evolution rate.

Evolution is influenced by

- Possibility to occupy different ecological niches (free habitats, habitat diversity)
- genetic variability and different speed of evolution in different systematic groups
- climatological changes (glaciations, changes during continental drift)
- geological changes (uplift, submersion, volcanism, break up or collision of continents)

- isolation (by islands, mountains, fragmentation of vegetation belts).

2.2.1 Neotropics

The numbers of bryophyte species recorded for a country give an impression of the floristic richness, the comparison with other countries also an impression of the state of exploration and the need for floristic activities.

As an example, the species numbers for various neotropical countries are:

Mosses:

- Mexico: 946 (Sharp et al. 1994)
- Colombia: 937 (Churchill & Linares 1995)
- El Salvador: 233 (Menzel 1991)
- Guyanas: 238 (Florschütz-de Waard 1990)
- Bolivia: 1222 (Hermann 1976)
- Ecuador: 783 (Steere 1948)
- Costa Rica: 542 (Bowers 1974)
- Venezuela: 626 (Pursell 1973), 1010 (Moreno 1992)
- Brazil: 3690 (Yano 1981)

Hepatics:

- Guyanas: 375 (Gradstein & Hekking 1989)
- Bolivia: 415 (Gradstein et al. 2003)

The present state of knowledge of the distribution of mosses in the neotropics is summarized in the database LATMOSS (Delgadillo et al. 1995). This catalogue indicated 4103 species and varieties in the neotropics. Due to taxonomic revisions, the number decreased to 3869 species and varieties (Delgadillo 2000), an effect, which will continue for the next time since many genera have not yet been revised. The exact number of hepatics is not known. 44% of the taxa of mosses are endemic. The highest rates of endemism are found in:

Brazil	46%
Bolivia	26%
Paraguay	26%
Ecuador	15%
Venezuela	13%
Peru	10%
Colombia	9%
Mexico	9%

Countries of low endemism rates are e.g. Guatemala, Belize, Honduras, Jamaica, the Guianas etc. The highest species numbers per area are found in Costa Rica (8.6 species per 10.000 km²)

This database allows comparison of the mossfloras of certain countries and checking the similarities. Of the 946 species of mosses in Mexico, and the 937 species in Colombia, 371 are identical. 241 of those 371 occur also in the West Indies. Thus it can be concluded that one third of the mossfloras of Mexico and Colombia is identical and that most of the species migrated from S to N.

The similarities of the bryofloras of the neotropical countries were calculated by Delgadillo (2000) by means of a cluster analysis, which nicely indicates the floristic subunits (Central America, Caribbean, Guianas, andine countries, Brazil.) and the level, on which the floras are related (at the present state of knowledge). Interestingly, Belize floristically belongs to the Caribbean, Honduras and Nicaragua are separated from the rest of Central American countries and Paraguay has a separate position between Chile/Argentina/Uruguay on the one and Brazil on the other hand.

The diversity of species varies much within a country in different altitudes. (see chapter on altitudinal zonation).

Diversity is also different in hepatics and mosses. According to Gradstein (1995), the tropical Andes have a hepatic flora of estimated 800 - 900 species. Most species are, however, in the upper montane belt above 2000 m, and the lower montane and subalpine forests have less species, although generally the species number of bryophytes raises with the elevation. There are also comparably many hepatic species in the lowland forests. The different diversity is determined by climatic, edaphic, physiological and phytogeographical factors.

Diversity differs not only within hepatics and mosses but also within different genera and families. Therefore spectra of families or genera are useful to determine differences between different regions or altitudes. In the Andes, montane forests have 2.5 much more hepatic families than lowland forests (Gradstein 1995). About 70% of all the species in lowland forests belong to the Lejeuneaceae. Reason is, that the majority

of bryophytes is characteristic for cool-temperate climates and that the colonization of the tropics in the Tertiary started from the cool temperate Gondwana flora (and to a smaller account from the northern hemisphere). For the Neotropics, the Andes provided a suitable pathway for immigration of taxa which subsequent speciation. Therefore the lowland taxa are relatively young adaptations to the physiological harsh conditions of tropical lowlands. The Lejeuneaceae adapted to this kind of new habitat with explosive radiation.

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2.2.2 Tropical Africa (contributed by T. Pócs)

Tropical Africa varies much in the level of the bryological exploration of its countries. The known number of species is summarized from the checklists of Hepaticae (Grolle 1995, Wigginton & Grolle 1996) and for Musci (O'Shea 1995). These lists reflect more the level of exploration of the different countries than their real species richness. Especially, there is a great discrepancy between the given species number and the size and habitat diversity of the concerned country (see maps and graphs in Pócs 1982, O'Shea 1997). Therefore, the country or island is marked in bold which is underexplored based on this discrepancy. The number of species is marked in bold, where the number of species is relatively high due to a reasonable high level of exploration.

	Hep.	Musci
Angola	58	125
Annobon	34	18
Ascensión	21	14
Benin	3	8
Bioko	58	122
Botswana	17	22
Burkina Faso	0	13
Burundi	88	69
Cameroun	223	361
Cabinda	0	2
Central Afr. Rep.	52	287
Chad	13	10
Comores	122	191

Congo (Brazzav.)	49	76
Congo (Zaire)	291	579
Cap Verde	30	113
Côte d'Ivoire	77	178
Equatorial Guinea	0	2
Eritrea	15	75
Ethiopia	119	285
Gabon	51	250
Gambia	1	1
Ghana	137	63
Guinea-Bissau	5	1
Guinea	53	196
Kenya	208	464
Liberia	3	55
Lesotho	22	163
Madagascar	354	751
Mali	2	15
Malawi	122	223
Mozambique	53	77
Namibia	31	56
Niger	0	6
Nigeria	133	141
Principe	24	14
Réunion	227	376
Rodrigues	16	35
Rwanda	223	293
South Africa	293	
Cape		389
Natal		340
Orange F.St.		137
Transvaal		299
Saô Tomé	84	74
Senegal	4	20
Seychelles	75	100
Sierra Leone	144	99
Socotra	12	25
Somalia	4	19
St. Helena	21	30
Sudan	10	31
Swaziland	21	89
Tanzania	389	780
Togo	33	83
Uganda	153	376
Zambia	59	141
Zimbabwe	135	265

From the above list it is easy to see where intensive research is still needed (the bold faced countries). The above data also suggest - where the ration between Hepaticae and Musci is

unusual - that one of them was properly investigated and the other component neglected. For example the Hepaticae of Ghana and Sierra Leone were much better explored by E.W. Jones and A.J. Harrington than the Musci by others. Pócs (1992) has further suggestions concerning the exploration of Hepaticae of the different countries.

South Africa is exceptional, where modern local floras elaborate the great part of Musci (Magill 1981, 1987, Magill & van Rooy 1998) and the thallose liverworts (many works of Perold) and not a too old flora (Arnell 1963) deals with all hepaticae.

For tropical Africa, quite a number of revisions are needed. The level of exploration is quite uneven comparing Hepaticae (thanks to the activities of E.W. Jones and C. Vanden Berghen) and Musci. Pócs & O'Shea compiled a list of basic taxonomic literature to identify tropical African bryophytes, which contain all revisions and monographs completed until that time, similarly to Greene & Harrington (1988), but trying to be more specific to Africa.

According to our present knowledge the number of Hepaticae in tropical and South Africa is 894 species. 713 occur on the continent and 436 on the Indian Ocean Islands, and 255 are shared between the two. For comparison: about 1250 species of hepatics occur in the neotropics. We do not even know the approximate numbers for tropical Asia.

As can be seen from the above list, there is much more to do for the taxonomy of Musci. At present, there are 3048 taxa recorded for the Subsaharan Africa (O'Shea 1997), which will be reduced to estimated 1300 by revisions. O'Shea (1997) deals in detail with the perspectives of African moss research.

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[Checklist of Malawi bryophytes](#)

[Checklist of mosses of sub-Saharan Africa](#)

[African mosses - diversity & endemism](#)

[Checklist of liverworts of sub-Saharan Africa](#)

2.2.3 Tropical SE-Asia

The bryoflora of SE-Asia is very diverse. The Indian subcontinent harbours a great deal of Laurasian taxa and therefore has with almost 1600 species the most taxa (cf. tab. 2.1). Also in Indochina, part of the 1000 species are possibly attributed from the Holarctic. The other parts such as Borneo or the Philippines have around 600 species, which is less than comparable regions in the Neotropics (e.g. in the Andes). The lowest species numbers are found in the densely populated lowland countries such as Bangladesh.

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Tab. 2.1: Number of mosses in SE-Asia

	No. of taxa	No. of endemics	% endemics	Ref.
Bangladesh	183	3	1.6	O'Shea 2003a
Pakistan	339	43	13	Higuchi & Nishimura 2003
Sri Lanka	561		11	O'Shea 2003b
India	1594	288	18	O'Shea 2003b
Indochina	1008	483	33	Tan & Iwatsuki 1996
Philippines	625			Tan & Iwatsuki 1991
Lesser Sunda Isl.	367			Touw 1992
Borneo	607			Touw 1978
Peninsular Malaya	475	20	4	Mohamed & Tan 1988

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2.3 Local diversity

Another important aspect is a determination of diversity on a small geographical scale. This can be done on different levels:

1. in different types of forests (primary - secondary forest, young secondary - mature secondary forest, lowland forest, montane forest), interior of forest, edge of forest, periodically flooded alluvial forest, episodically flooded forest.
2. on different types of habitats (trunk epiphytes, canopy epiphytes, soil, disturbed soil, rocks, leaves.
3. systematic diversity: percentage of families in different regions, vegetation types or habitats. Percentage of endemism.
4. succession studies in different old regrowths. The results of such studies give answers to questions such as:
 - which are the most species rich vegetation types?
 - Which vegetation types need therefore the most regard with respect to nature conservation?
 - Which species are lost by destruction of vegetation types e.g. primary forests?
 - Which species are indicators of primary forests and need therefore to be placed in red lists?
 - Which species can survive in secondary habitats?
 - Which species occur only in secondary habitats and are indicators of these habitats?
 - Which species are indicators of disturbed, man-made habitats? (Serrano 1996).
 - Which species can be used for determination of altitudinal belts?

As expressed above, bryophytes are easier tools for answering such questions than flowering plants because they are less numerous, better indicator species because of their physiology of water and nutrient uptake (e.g. for climatic conditions) and easier to be identified.

The low number of bryophyte species worldwide does not result in a low local species diversity. In a lowland forest in French Guiana, Montfort & Ek (1990) found 154 species of bryophytes (66 mosses, 88 hepatics) on 28 trees representing 22 species. Four to five trees yielded about 75% of the total number of bryophyte species. In a drier type of lowland forest, Cornelissen & ter Steege (1989) found 79 bryophyte species (26 mosses, 53 hepatics).

Wolf (1993) found between 55 and 140 species of bryophytes in a set of each four trees in elevations between 1500 and 3500 m.

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3. ORIGIN AND AGE OF TROPICAL BRYOPHYTES

It should be stressed that mosses have undergone reduction during their evolution. The oldest fossils were always costate and probably acrocarpous. Ecostate and pleurocarpous taxa have apparently developed only later, as an adaptation to ecological niches in the understory of forests in the Tertiary. Insofar, tropical bryophytes are predominantly the youngest branch of evolution. Recent results of molecular studies show that some (of not many) are derived from Gondwanalandic ancestors.

We know nothing about the phylogenetic origin of bryophytes, thus their ancestors remain unknown. In the past, bryophytes were derived from algae and pteridophytes from bryophytes, because of „Haeckel's law“ (the ontogeny repeats the phylogeny). It was argued that bryophytes share an algal stage (the protonema) in their ontogeny and pteridophytes a bryophyte stage (the prothallium). Accordingly, the organisation of mosses was and is commonly still regarded as thallophytic in many textbooks of botany. The oldest known bryophyte fossil is *Pallavicinites devonicus* from the Devonian of North America. It resembles the extant thalloid liverwort genus *Pallavicinia* (similar to the tropical genus *Symphyogyna*). Therefore bryophytes have evolved even earlier and we have no fossil evidence for the origin. It can, however, be concluded from the drastic anatomical and morphological differences between liverworts, hornworts and mosses that these groups may not be monophyletic. It can be argued that mosses as well as hornworts have developed from primitive tracheophytes by reduction, since they show several cormophytic characters such as stomata in the sporophyte, a cuticula and also conducting tissues, which are no more functional and probably remnants of tracheophytic ancestors. The stomata are no more needed but originated surely in plants in which they were

functional. Thus the sporophyte of mosses is principally not dissimilar to sporophytes of ferns (although it is not independent). This allows speculations about the origin of mosses and hornworts from primitive tracheophytes but clearly not from algae.

Similar cormophytic structures are found in the stems of Polytrichaceae with a highly developed conducting system. With an internal hadrom and an external leptom, it resembles the conducting system of fossil Psilophytales. Even the leaves possess highly organized conducting tissues. However, the leaf traces have no connection with the central stem. This can also only be explained as reduction. Therefore bryophytes must be regarded as reduced tracheophytes.

3.1 Evidence from fossils

The fossil history of bryophytes is not well known because only relatively few fossil bryophytes have been found. During the 19th century, fossil bryophytes were only known from Quaternary and Tertiary and it was said that bryophytes cannot be preserved as fossils since they lack lignine.

In 1959, Savicz-Ljubitskaja & Abramov knew 33 species of bryophytes from the Palaeozoic and Mesozoic, and Jovet-Ast (1967) raised the number to 68. The most recent survey of bryophytes of the Mesozoic and Palaeozoic was compiled by Oostendorp (1987).

The Devonian bryoflora consisted of thalloid liverworts (Metzgeriales) and probably also a hornwort. First mosses were found in Carboniferous deposits. The richest source of fossils from the Palaeozoic is known from the Permian of Russia and Antarctica. These mosses resemble extant taxa of the order Bryales. Permian deposits have also revealed the first leafy

liverwort and the first moss with a differentiation of chlorocysts and hyalocysts, as in extant *Sphagna*, although with a different habit.

Mesozoic fossils are rich in Marchantiales, e.g. plants similar to *Marchantia* and *Riccia*, showing adaptations to dry climates.

The fossil bryophytes of the Tertiary from Europe and North America, and also all fossils from the Quaternary, are almost all extant species (Gams 1932, Dickson 1973, Miller 1984).

The best fossil from the Tertiary are preserved in amber. Tertiary amber is known from Europe, the island of Hispaniola (Dominican Republic) and Mexico. The European amber was produced by pine trees in pine-oak forests in present Scandinavia in the Eocene. The resin flew over epiphytic bryophytes or single bryophytes were blown in the resin by wind. The forest was drowned by raising sea level, the resin was washed out and transported to the region of the former Eastern Prussia, today Russia, south of the Baltic countries, and is called Baltic amber. From there it was partly transported to Saxony in Germany (called Saxon amber) and widely dispersed by glaciation during Quaternary.

Amber is the greatest source of fossil bryophytes since the plants are perfectly preserved. Even oil bodies are preserved in hepatics (Grolle & Braune 1988). The hepatics in amber were studied by Grolle (1983). He listed 18 species from Baltic and Saxonian amber and 12 species from Dominican and Mexican amber.

The earliest bryophyte fossils from the neotropics are found in Dominican and Mexican amber from the Tertiary with an age of 25-45 mio years. The fossil hepatics were studied by Grolle (1983, 1984a, 1984b, 1985, 1987, 1988, 1990, 1993). Grolle described all fossil hepatics as extinct species in extant genera. Therefore speciation of hepatics must have happened during the last 25-45 mio years. Gradstein (1993) reported 10 hepatics from Dominican amber, of which 3 could be recognized as extant species.

The mosses in Dominican amber were studied by Frahm (1993, 1994, 1996). Altogether 11 species of mosses could be identified: *Adelothecium bogotense*, *Clastobryum* sp., *Homalia* sp., *Hypnum* sp., *Mittenothamnium* sp., *Neckera* sp., *Octoblepharum* cf. *pulvinatum*, *Pilotrichella* sp., *Syrrophodon africanus* ssp.

graminicola, *S. incompletus* var. *incompletus*, and *Thuidium erectum*. All these genera and species are still existing on the island of Hispaniola (the origin of Dominican amber). These are all genera and species which are widely distributed in the neotropics. It shows that the main stock of mosses in the neotropics was already present in the Tertiary and that these species are at least 25-45 mio years old. Also the fossil bryophytes in Baltic and Saxon amber are of interest for tropical bryology, since the climate in Oligocene and Miocene was subtropical in Scandinavia. Therefore Baltic amber contains many subtropical elements. Again, the fossil hepatics were identified as extinct species of extant genera but with phylogeographical relationships to the subtropics, especially of E-Asia. The fossil mosses consist in part of extinct species, in part of extant species. The moss flora of the amber forest was composed by species of *Barbella*, *Hypnum*, *Campylopus*, *Campylopodia*, *Fabronia*, *Haplocladium* and others. The most common epiphyte was *Hypnodontopsis confertus* (Frahm 2001) described in the 19. century from amber as *Muscites confertus* but in 1928 from an extant collection as *Hypnodontopsis mexicana* from Mexico. The present rarity (the species was found additionally only in Uganda) indicates that the formerly common species is getting extinct at present. Many species are still found in pine oak forests; they have kept their habitat over millions of years.

In conclusion, tropical genera were already existing in Tertiary and even many species at least amongst the mosses were present 25-45 mio years ago, giving an estimate of the age of species. This does not mean that all bryophyte have that age. There are certainly younger species (e.g. mountain endemisms) and probably also older (see chapter on molecular evidence).

Dickson, J.H. 1973. Bryophytes of the Pleistocene. Cambridge.

Frahm, J.-P. 1993. Mosses in Dominican amber. Journal of the Hattori Botanical Laboratory 74: 249-259.

Frahm, J.-P. 1994. Moose - lebende Fossilien. Biologie in unserer Zeit 24: 120-124.



Fig. 3.1: *Syrrhopodon incompletus* in Dominican amber.

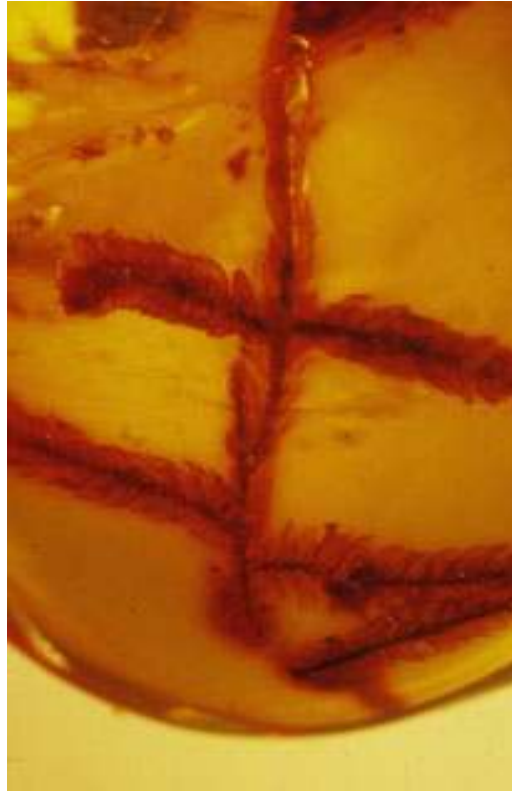


Fig. 3.2: *Pilotrichella* sp. in Dominican amber.

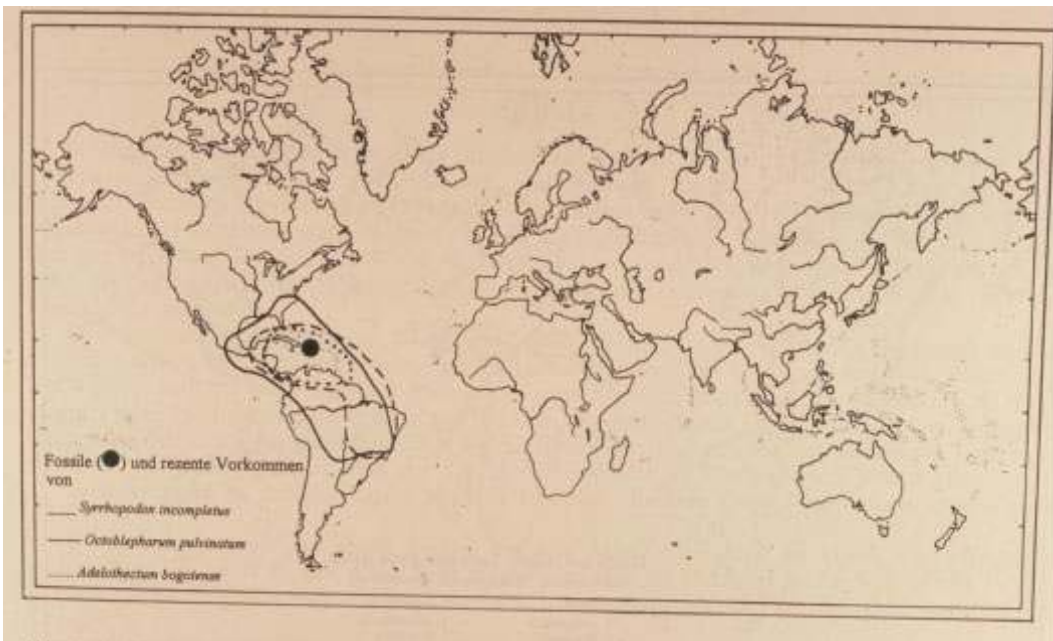


Fig. 3.3: ranges of moss species found in Dominican amber.

- Frahm, J.-P. 1996.** New records of fossil mosses from Dominican amber. *Cryptog. Bryol. Lichénol.* 17: 231-236.
- Frahm, J.-P. 1996.** New records of fossil mosses from Dominican amber. *Cryptogamie, Bryologie Lichénologie* 17(3): 231-236.
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- Frahm, J.-P. 2001.** New records of mosses from Dominican amber. *Tropical Bryology* 20: 39-42.
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- Grolle, R. 1983.** *Leucolejeunea antiqua* n.sp., das erste Lebermoos aus Dominikanischem Bernstein. *Stuttgarter Beitr. Naturk. Ser. B*, 96: 1-9.
- Grolle, R. 1984a.** *Bryopteris* and *Cyclolejeunea* fossil. *J. hattori Bot. Lab.* 56: 271-280.
- Grolle, R. 1984b.** *Cyrtolejeunea suzannensis* spec. nov., ein weiteres fossiles Lebermoos in dominikanischem Bernstein. *Cryptogamie Bryol. Lichénol.* 5: 27-32.
- Grolle, R. 1985.** *Lejeunea palaeomexicana* n.sp. *Stuttg. Beitr. Naturk. Ser. B.* 108: 1-7.
- Grolle, R. 1987.** *Radula steerei* sp.nov., a further hepatic in Dominican amber. *Mem. N.Y. Bot. Gard.* 45: 259-263.
- Grolle, R. 1988.** Bryophyte fossils in amber. *Bryol. Times* 47: 4-5.
- Grolle, R. 1990.** *Leucolejeunea antiqua* (ein Lebermoos aus Dominikanischem Bernstein) erstmals mit Gynözium, Perianth und Andrözium. *Nova hedwigia* 90: 101-108.
- Grolle, R. 1993.** *Bryopteris bispinosa* spec. nov. (Lejeuneaceae), ein weiteres Lebermoos aus dominikanischem Bernstein. *J. Hattori Bot.Lab.* 74: 71-76.
- Jovet-Ast, S. 1967.** Bryophyta. In: E. Boureau (ed.), *Traite de Paléobotanique* 2:17-186. Paris.
- Miller, N.D. 1984.** Tertiary and Quaternary fossils. In: R.M. Schuster, *New Manual of Bryology*: 1194-1232. Nichinan.
- Oostendorp, C. 1987.** The bryophytes of the Palaeozoic and Mesozoic. *Bryophyt. Biblioth.* 34: 1-112, XLIX pls.
- Savicz-Ljubitskaja, L.I. & Abramov, I.I. 1959.** The geological annals of Bryophyta. *Revue Bryol. Lichénol.* 28:330-342.

3.2 Evidence from plate tectonics

Since there are only few fossils known, especially from the Mesozoic and Palaeozoic, and the structures preserved in the fossils rarely allow a detailed examination, the age of bryophytes can be concluded from their geographic ranges.

How old are tropical bryophytes ?

We have evidence from Gondwanalandic ranges that certain bryophyte species were in existence already 135 mio years ago. There are species, which are not only disjunct between SE-Brazil and SE-Africa but the same species occur also in Sri Lanka and southern India (fig. 3.6). This type of disjunction cannot be explained by long distance dispersal. Also certain species in common in tropical Africa and in the neotropics, which lack effective means of long distance dispersal or which are not able for long distance dispersal because of lacking UV and frost tolerance, are probably of a comparable age. Rain forests, as we know them today, originated in the beginning of the Tertiary; they are thus less than 70 Mio years old. Thus we can assume that tropical lowland species originated about at this time. The tropical montane bryoflora is derived from invasions from the holarctic and, mainly, from the subantarctic. Many species (e.g. *Lepyrodon tomentosus*) which are widely distributed through New Zealand, Tasmania and Chile go up to the Andes. During this migration, speciation has taken place as adaptation to new habitats. Such genera (e.g. *Chorisodontium*) are subantarctic in origin but have secondary centers of evolution in the tropical mountains. *Campylopus* is represented in the subantarctic

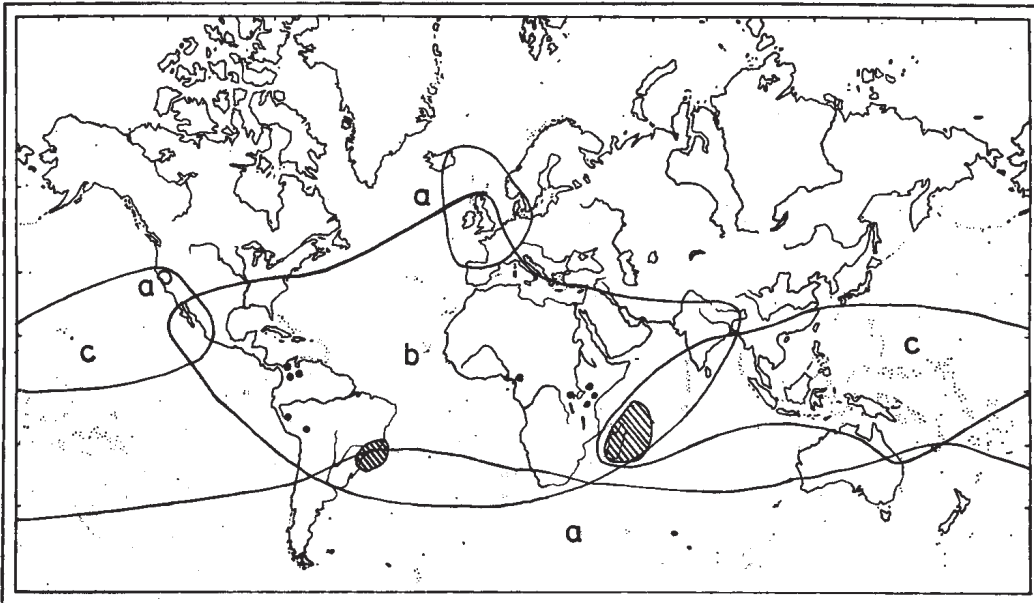


Fig. 3.4: Distribution of a. *Campylopus introflexus*, b. *C. pilifer*, c. *C. aureus* and *C. julaceus* (hatched). *C. introflexus* can be regarded as ancestor, *C. pilifer* and *C. aureus* migrated into the tropics, *C. pilifer* presumably at a time when the Gondwana continent was intact. *C. julaceus* lived along the S-coast of the Gondwana continent and its range was split.

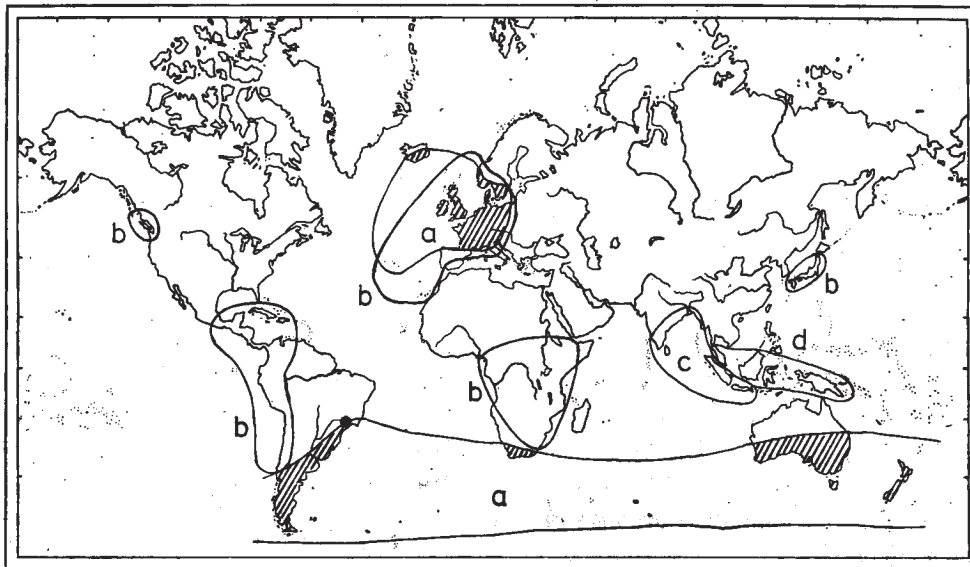


Fig. 3.5: Distribution of *Campylopus pyriformis* (a), *C. fragilis* (b), *C. zollingerianus* (c) and *C. crispifolius* (d). *C. pyriformis* can be regarded as ancestral species, from which the others developed.



Fig. 3.6: Range of *Campylopus controversus* as example of a gondwanalandic range. The disjunct occurrence in eastern south America, SE-Africa, the East African Islands and Sri Lanka is explained as former continuous range.

with 14 species, but has 40 species in the northern Andes, which may be derived from subantarctic ancestors. Thus the youngest species in evolution are those from young mountain systems with an age of 10 (New Guinea) or only 3 (the Andes) million years.

Most of the bryophyte species are found on tropical mountains: species numbers as well as phytomass increases with elevation. This is due to the physiology, which resembles that of temperate bryophytes.

Pathways of migration from the subantarctic to the tropics were:

- the Andes, which provide a continuous migration route. This is the reason why the neotropics has the highest species numbers and diversity.
- the mountains of tropical Africa, which could only be reached by "mountain hopping".
- "Noahs arc"; species which lived on the Indian continent, when it was part of the Gondwana continent, and drifted on the Indian plate northwards. There are disjunctions between Madagascar and southern India /Sri Lanka, which show that at least part of the species survived the long trek. However, some of the species migrated

into SE-Asia from India and have partly undergone explosive speciation. Another pathway was detected very recently (Vitt 1990): SE-Asia was also colonized by bryophytes from Australia.

Similar young species are found as endemics on young volcanic islands, although many of them have turned out, or will turn out, in world wide revisions to be more widespread., e.g. reductions of endemic species of *Campylopus* in Hawaii (Frahm 1991) or in New Caledonia (Frahm 1990).

Bryophytes have a special role as indicators of continental drift since they are much older than flowering plants. The disjunctions of flowering plants concern genera, those of bryophytes species!

Frahm, J.-P. 1990. A short survey of the *Campylopus* flora of New Caledonia. Cryptog. Bryol. Lichénol. 11: 369-375

Frahm, J.-P. 1991. A survey of the *Campylopus* flora of Hawaii. Bryologist 94: 60-66.

Vitt, D.H. 1990. *Desmotheca* (Orthotrichaceae): Gondwanan fragmentation and the origin of a Southeast Asian genus. Trop. Bryol. 3: 79-88.

4. MORPHOLOGICAL ADAPTATIONS

The morphology of plants is to be understood as a reaction upon environmental factors and therefore it can be used to characterize different ecological conditions. Analysis of the morphology is especially helpful in comparisons of different habitats or in studies of different relevés along a gradient, e.g. an altitudinal transect. Even if the species are not exactly known, an analysis of morphological adaptations provides useful insights in the altitudinal zonation of rain forests. The adaptations concern morphology and anatomy.

4.1 Life and growth forms

Giesenhagen (1910) was the first to define „Moostypen“ in rain forests in SE-Asia, which were types of growth forms.

Both the morphological features of individual bryophyte plants as well as the appearance of aggregated individuals have been used, for which the terms life form and growth form have been used. However, there is even still much confusion in terminology. Meusel (1935) was the first to introduce a system of **growth forms** of mosses based on branching patterns. He distinguished between orthotropous and plagiotropous mosses with subforms. Gimingham and Birse (1957) elaborated a system of growth forms for temperate mosses and Birse (1957) tested it experimentally. They described the general appearance of colonies. For Mägdefrau (1969, 1982), growth form is a morphological feature of a single plant (e.g. plagiotrop, orthotrop) and

life form is the composition of individuals (e.g. in tufts or mats). Mägdefrau's life form system, however, includes also types of individuals (e.g. tails, dendroids) together with types of colonies (mats, cushion etc.). Mägdefrau also distinguished annuals, short turfs, tall turfs, cushions, mats, wefts, pendants, tails, fans, and dendroids. It must be noted that annual is today not regarded as a life form but a life strategy (annual vs. perennial).

In practice, it is hardly possible to see any exact distinction between short turf and tall turf (which are now combined) and the distinction between fans and tails seems to be superfluous. Therefore the system is modified by almost every author. The system used in various studies during the BRYOTROP projects is the following (fig. 4.1):

crusts
wefts
mats
fans
cushions
turfs
pendants
dendroids

It is clear that life forms are adaptations to special ecological niches and reflect habitats. They are especially related to moisture conditions (Tobiessen et al. 1977, Pócs 1982, Thiers 1988, Proctor 1990).

Life forms have successfully been used to recognize altitudinal belts in rain forests of SE-Asia (Frey et al. 1990), Central Africa (Frey et

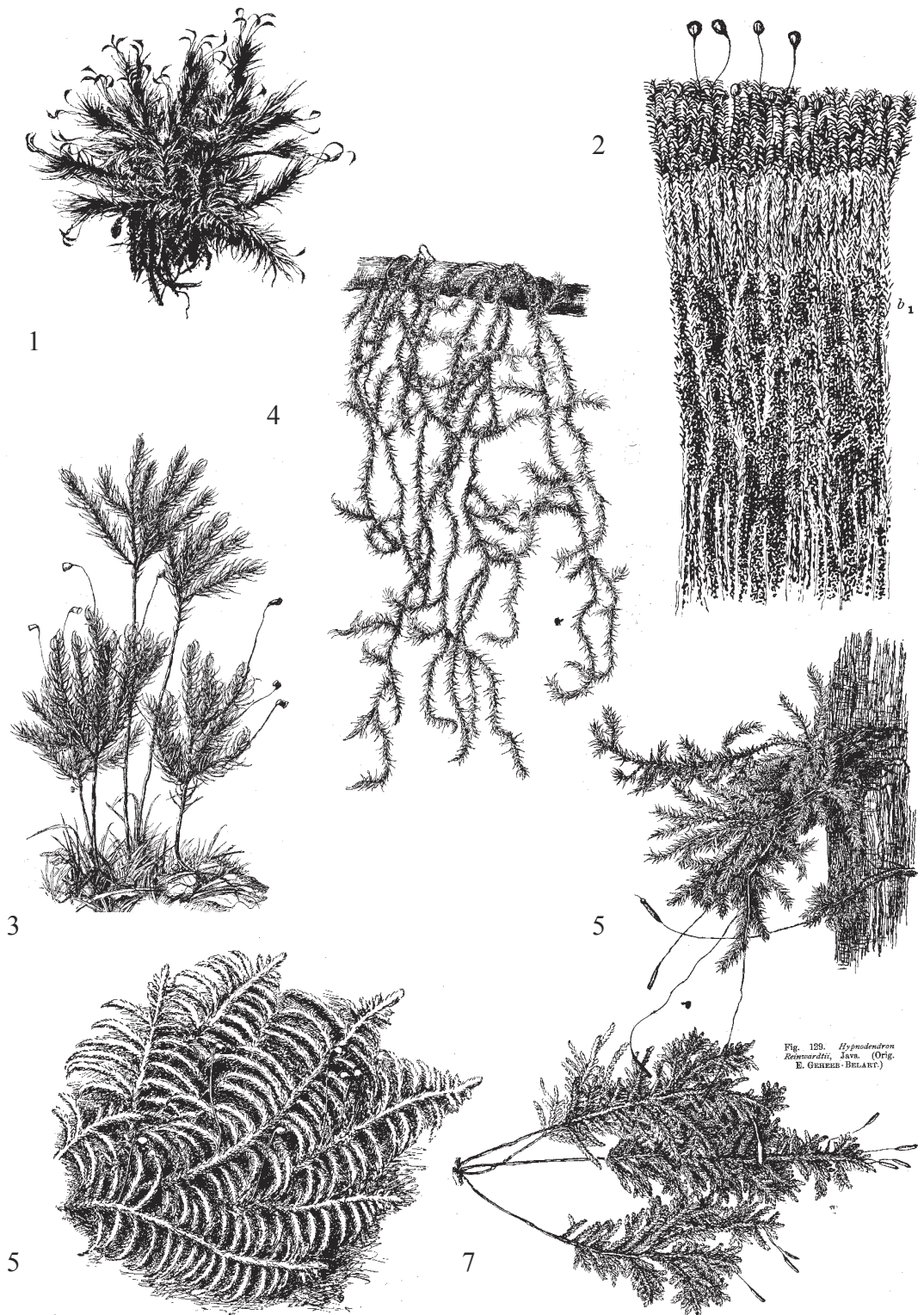


Fig. 4.1: Life forms of mosses: 1. turf, 2. cushion, 3. dendroid, 4. pendant, 5. tail, 6. mat, 7. fan.

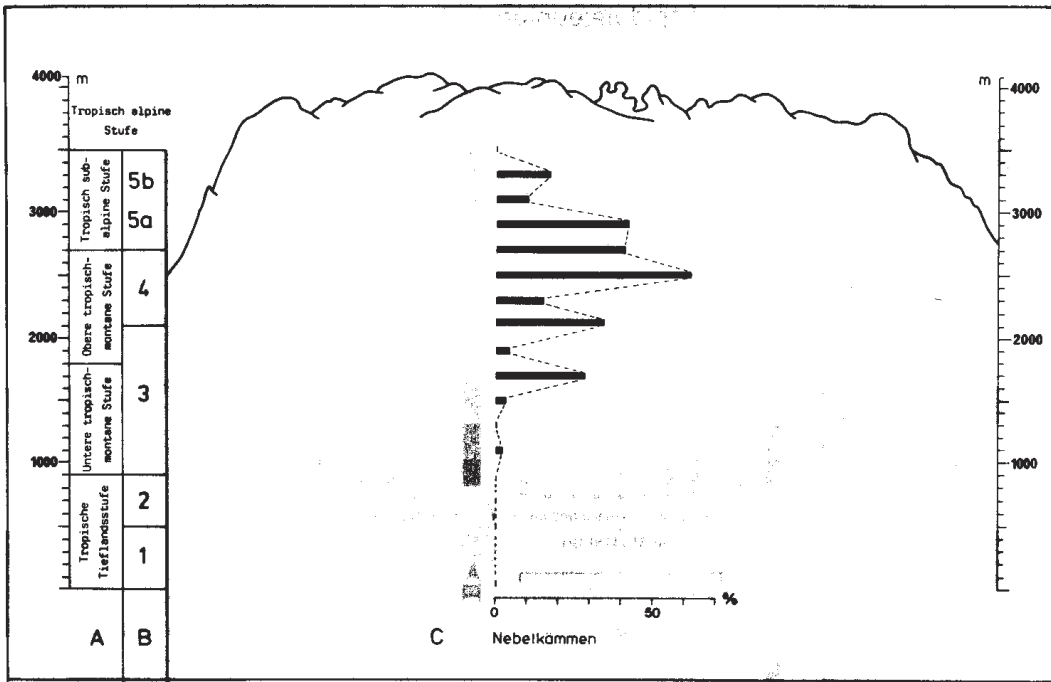


Fig. 4.2: Distribution of pendants along a transect on Mt. Kinabalu, Borneo (from Frey et al. 1990)

al. 1995) and the Andes of Colombia (Groot et al. 1993). Along altitudinal transects, crusts (of hepatics such as Lejeuneaceae) are highly characteristic for lowland forests, wefts and fans are typical for montane forests, whereas wefts and mats are found at higher altitudes. Subalpine regions are rich in cushions, turfs and mats (fig. 4.2).

In general, mats, wefts and cushions are particularly effective in storing water and are characteristic for habitats with occasional desiccation. Pendants are highly characteristic of cloud belts, since this life form can effectively „comb“ humidity from mist. Dendroids are intolerant of longer periods of desiccation, since the internal conducting system is not effective enough to transport water to the upper parts of the plant. Tails and fans seem to be an adaptation for a better gas exchange and to avoid to be wetted along tree trunks, which reduces gas exchange.

Birse, E.M. 1957. Ecological studies on growth form in bryophytes. II. Experimental studies in growth forms of mosses. *J. Ecol.* 45: 721-733.

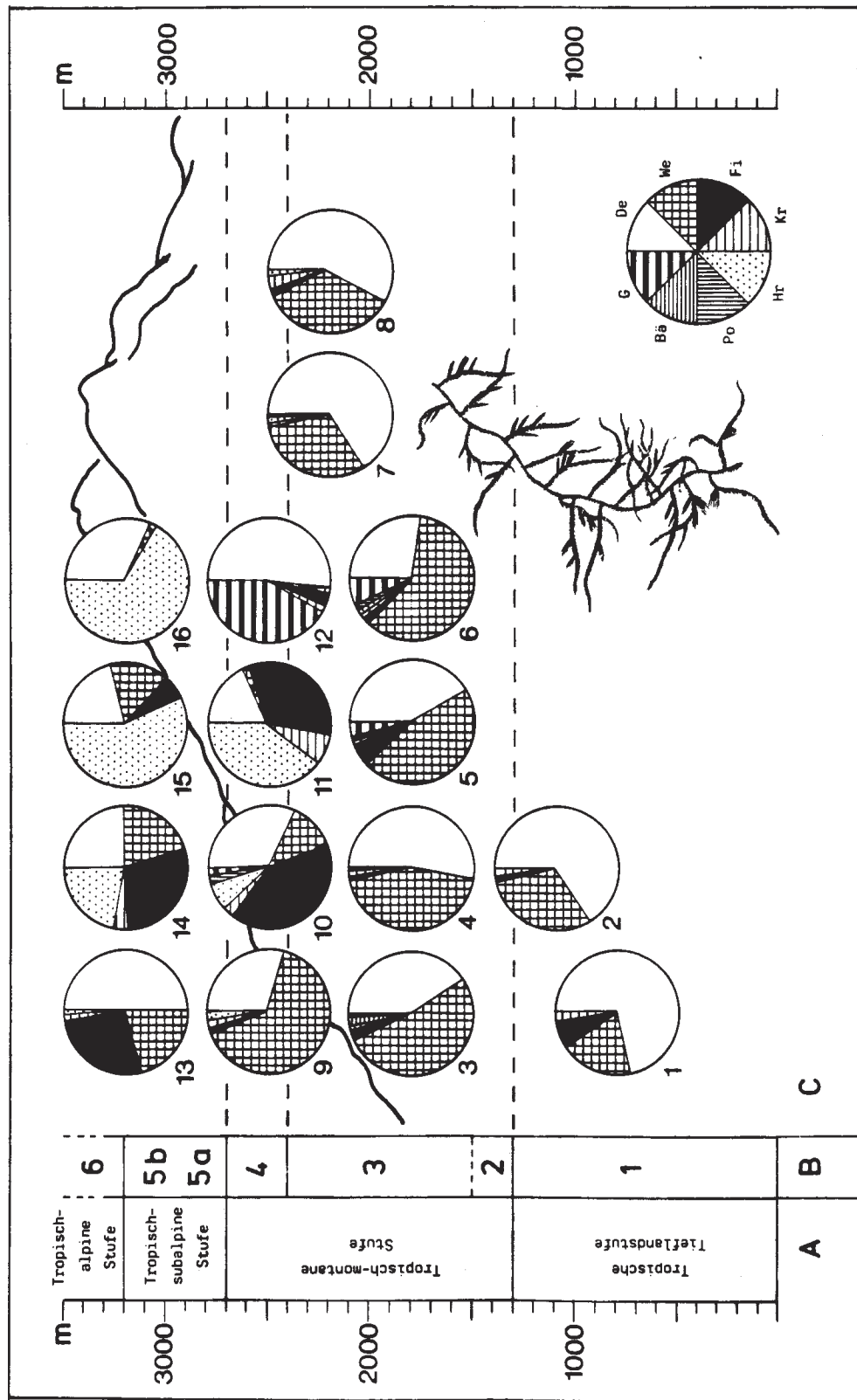
Frey, W., Gossow, R. & Kürschner, H. 1990. Verteilungsmuster von Lebensformen, wasserleitenden und wasserspeichernden Strukturen in epiphytischen Moosgesellschaften am Mt. Kinabalu (Nord Borneo). *Nova Hedwigia* 51: 87-119

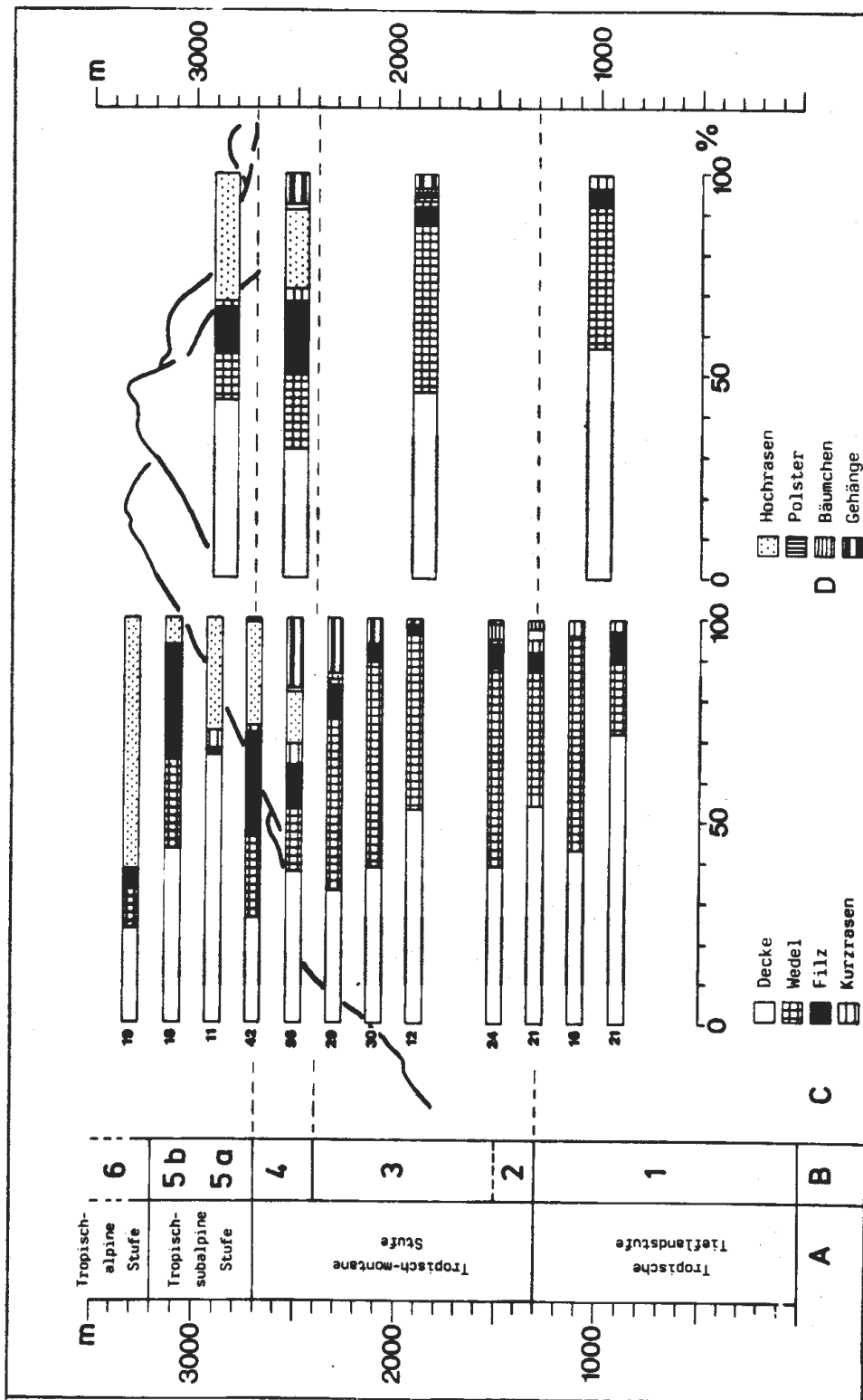
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Gimingham, C.H., Birse, E.M. 1957. Ecological studies on growth form in bryophytes. I. Correlations between growth form and habitat. *J. Ecol.* 45: 533-545.

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- Pócs, T., 1982.** Tropical forest bryophytes, In: A.J.E. Smith (ed.), *Bryophyte Ecology*, pp.59-104. London
- Proctor, M.C.F. 1990.** The physiological basis of bryophyte production. *Bot. J. Linn. Soc.* 104: 61-77.
- Thiers, B.M. 1988.** Morphological adaptations of the Jungermanniales (Hepaticae) to the tropical rain forest habitat. *J. Hattori Bot. Lab.* 64: 5-14.
- Tobiessen, P.L., Mott., K.A., Slack, N.G. 1977.** A comparative study of photosynthesis, respiration and water relations in four species of epiphytic mosses in relation to their vertical distribution. *Bryoph. Biblioth.* 13: 253-277.

4.2 Water conducting and water storing structures

The use of life forms as indicators of environmental factors, especially the humidity factor, is based on morphological characters. In the same way also anatomical structures are adapted to the water factor, since the period in which the plants are turgescient is also the period for photosynthesis. The water conducting structures enable the plant to take up water rapidly (within seconds) and to start photosynthesis immediately.

Anatomical adaptations related to water conducting and water storing are:

1. Presence of a central strand

Central strands are present in many acrocarpous mosses. They consist of a „hadrom“ consisting of narrow, elongated cells with oblique end walls. This hadrom can conduct water but not sufficiently. If external water conduction is interrupted (e.g. by shaving the rhizoids and leaves from the stem) the moss dries up. However, the central strand contributes to water conduction a certain amount. Mosses with a central strand are growing on humid substrates but are exposed to frequent desiccation.

2. Presence of external water conduction

External conduction of water is made possible by a tomentum of rhizoids along the stem and by concave leaves in which the water is conducted by capillarity. A tomentum is characteristic for mosses growing on wet, exposed substrates (e.g. *Philonotis* on dripping cliffs). Concave leaves are typical of pleurocarpous mosses with a prostrate growth.

3. Papillae on the leaf surface

Papillae enable the plant to soak water rapidly over the leaf surface. This can easily be tested by putting two dry plants, one with a papillose leaf lamina and one with a smooth leaf lamina, in water. The papillose leaf will be wetted immediately. In addition, water can also be stored between the papillae.

4. Water sacks

Water sacks are especially characteristic of certain groups of hepatics. In Scapaniaceae, Radulaceae and Lejeuneaceae, the lower part of a leaf is folded upwards and forms a „gab“ of different size in which water can be stored. The highest differentiation of this mechanism is found in the genus *Frullania*, in which this lower part of the leaf is separated and forms a closed bottle- or cup-like structure.

5. Alar cells

Alar cells are cells at the basal angles of the leaves of certain mosses. They are found in acrocarpous mosses (e.g. Dicranaceae) as well as, and more

Figs. 4.3-4.4 on p. 30-31: Distribution of life forms along a transect on Mt. Kinabalu, Borneo (from Frey et al. 1990)



Fig. 4.5: Water conducting and storing structures of bryophytes. 1-2. Alar cells (*Sematophyllum brachytheciiiforme*), 3-5. Concave leaves 3. *Marchesinia excavata*, 4. *Evansiolejeunea roccatii*, 5. *Pilotrichella profusicaulis*. 6-9. Ciliate leaves. 6-8. *Herbertus doggeltianus*, 9. *Leptoscyphus infuscatus*. 10. Hyalocysts (*Campylopus nivalis*). From Kürschner & Seifert 1995..

frequently, in pleurocarpous mosses (e.g. Hypnaceae, Amblystegiaceae Brachytheciaceae, and especially Sematophyllaceae). They can be firm-walled, incrassate and usually reddish coloured, but more often thin-walled and inflated. They function in absorbing water into the leaf, which is externally conducted along the stem by rhizoids or concave leaves.

6. Cilia

Bryophyte leaves are organs for water uptake (in addition to photosynthesis, of course). In the hepatics, the leaves can be incised one to several times and form acute lobes. The apices can be condensation points for humidity. If the leaves are split partially at the margins (e.g. *Trichocolea*) or totally (*Kurzia*, *Blepharostoma*) to form single cell-rows (cilia), these structures enlarge the surface of the leaves drastically and facilitate absorption of water.

7. Hyalocysts

Hyalocysts are large, empty, dead cells in the leaves of some moss families such as Sphagnaceae, Dicranaceae (*Paraleucobryum*, *Campylopus*) and Calymperaceae, rarely also in some genera of Pottiaceae (*Tortula*, *Tortella*). They can store large amounts of water, and are therefore interpreted as water storing structures, although many of them grow characteristically in damp habitats, where storage is not necessary. Water storing and conducting structures were successfully used for an altitudinal zonation of bryophytes in rain forests in Peru (Frahm 1987), Borneo (Frey et al. 1990) and Central Africa (Kürschner & Seifert 1995).

In Zaire and Rwanda, bryophyte species with cilia or hyalocysts occurred only at higher elevations (high montane, subalpine and alpine belt). Species with a central stand and a rhizoid tomentum were mainly found above 2000 m, whereas papillose and mamilllose leaf surfaces were found at all elevations .

Frahm, J.-P. 1987. Struktur und Zusammensetzung

zung der epiphytischen Moosvegetation in Regenwäldern NO-Perus. Beih. Nova Hedwigia 88: 115-141.

Frey, W., Gossow, R. & Kürschner, H. 1990. Verteilungsmuster von Lebensformen, wasserleitenden und wasserspeichernden Strukturen in epiphytischen Moosgesellschaften am Mt. Kinabalu (Nord Borneo). Nova Hedwigia 51: 87-119

Kürschner, H. & Seifert, U.H. 1995. Wissenschaftliche Ergebnisse der BRYOTROP Expedition nach Zaire und Rwanda 6. Lebensformen und Adaptationen zur Wasserleitung und Wasserspeicherung in epiphytischen Moosgesellschaften im östlichen Kongobecken. Trop. Bryol. 11: 87-118

4.3 Life strategy

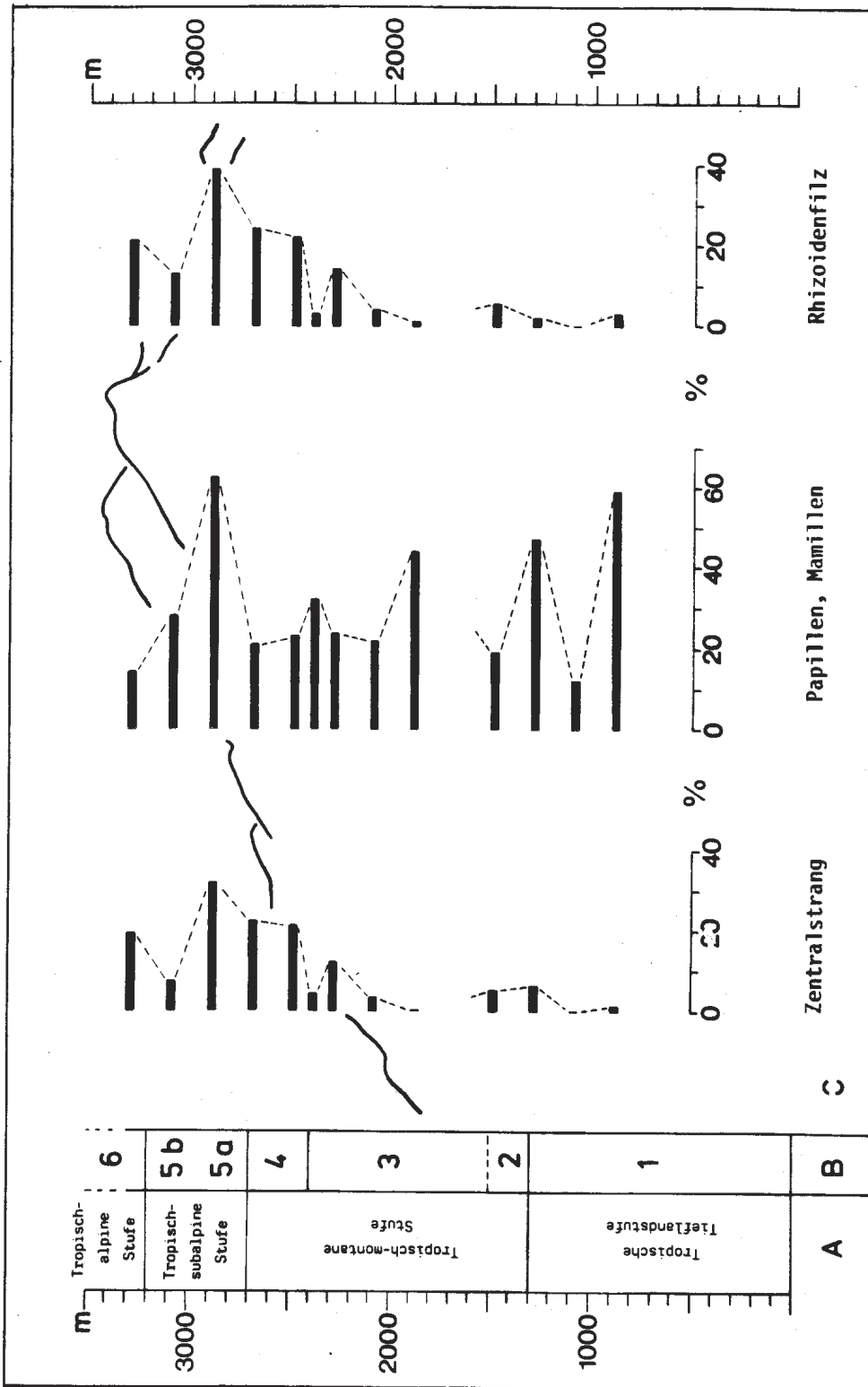
Under the term life strategy the different life histories of bryophytes are understood. The term life strategy makes not much sense since a strategy means a adaptation to changing conditions. This is not the case in genetically fixed life cycles. During (1979) distinguishes between:

Fugitives
Colonists
Annual shuttle species
Short lived shuttle species
Perennial shuttle species
Perennial stayers

Life strategies are adaptations of the life history to different habitats. They concern primarily the length of the life cycle (ephemeral, annual to perennial) but also different types of reproduction (sexual, asexual), spore size and growth form.

During, H. J. 1998. De diasporenvorraad in de bodem van een savanne in

Fig. 4.6: Distribution of water conducting structures along a transect on Mt. Kinabalu, Borneo (from Frey et al. 1990).



- Zimbabwe. *Bauxbaumiella* 45: 2-13.
- During, H. J., and C. Moyo. 1999.** The diaspore bank of bryophytes in a Zimbabwean savanna. *Haussknechtia Beiheft (Ricleft Grolle-Festschrift)* 9:111-114.
- Frey, W., and H. Kürschner. 1991.** Lebensstrategien epiphytischer Bryophyten im tropischen Tieflandsund Bergregenwald am Mt. Kinabalu (Sabah, Northern Borneo). *Nova Hedwigia* 53:307-330.
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- Olarinmoye, S. O. 1986.** Aspects of survival strategies in three common mosses in Ibadan, Nigeria. *Cryptogamie, Bryologie, et Lichénologie* 7:213-218.
- Van Leerdam, A., R. J. Zagt, and E. J. Veneklass. 1990.** The distribution of epiphyte growth-forms in the canopy of a Colombian cloud forest. *Vegetatio* 87:59-71.
- Zander, R. H., and H. J. During. 1999.** *Neophoenix* (Pottiaceae), a new African moss species found through soil diaspore bank analysis. *Taxon* 48:657-662.

5. ECOLOGY OF TROPICAL BRYOPHYTES

5.1 Habitats

The bryophyte habitats in the tropics are much different from those in temperate, boreal or arctic regions. Predominant vegetation type is the forest. Within the forest, the soil is not much covered by bryophytes due to the large amount of litter and its fast decomposition. This is especially true for lowland forests, where only rarely small quantities of Fissidens are found on bare soil and a few bryophytes on termite nests and ant gardens. The amount of bryophytes on soil is slightly increasing in montane forests with increasing elevation, especially along roadside banks (there are no bryophytes along roadside bank in the lowlands!) and forests floors covered by bryophytes are only found in the subalpine. Furthermore, there are usually no rocky habitats at lower altitudes in the humid tropics due to the deep lateritic soils and fast chemical decomposition. This confines the variety of habitats in rain forests areas mainly to trees and their leaves.

5.1.1 Epiphytes

The high to immense quantity of epiphytic bryophytes is a special character of (temperate and tropical) rain forests. It is a direct result of the high humidity. High humidity means that the

poicilohydric bryophytes are almost all the time photosynthetic active. The longer the light period, in which bryophytes are wet, the higher is the net-photosynthesis (right temperature and light conditions presupposed) and the higher is the production of phytomass. Furthermore, humidity provided by rain supports nutrients, and the more rain the more nutrients get the bryophytes. The effect, that bryophyte phytomass increases with elevation by higher humidity and increasing precipitation can also be observed in mountains of temperate regions, where the mass of epiphytic bryophytes can reach the amount of rain forests in relatively dry regions or not too high elevations (Frahm 2002).

Epiphytic bryophytes are very sensitive to habitat factors such as bark structure, bark pH, microclimate. The fact that they are exclusively supplied with water and nutrients from the atmosphere makes them to excellent bioindicators for air quality, which has been often used in Europe but so far only to a small extent in tropical countries (cf. chapter 8).

The tree habitat for epiphytes is very different concerning its microhabitat conditions. Previous authors such as Richards (1984, 1991) differentiated between shade and sun epiphytes. Therefore the tree is usually divided into several zones (trunk, canopy with inner and outer

branches and twigs). The most widely used classification is that by Johannson (1974), see fig. 5.1.

The bryophyte flora (as well as the flora and fauna in general) of the canopy has formerly much been neglected. Canopy studies were usually confined to fallen trees. Since 25 years, alpine climbing techniques, canopy walks, cranes (figs. 5.3, 5.4) and airships make canopy studies possible. Especially climbing techniques and crane studies have enhanced the knowledge of the bryoflora of the canopy.

The epiphytic bryophyte species of shady habitats are more vulnerable to forest destruction and disappear soon when the forest is opened. They are good indicators for primary forests. Canopy bryophytes are, however, more tolerant to desiccation. They are also found epiphytic in open habitats, e.g. savannahs and plantations. Therefore primary forests are more species rich than secondary forests.

The epiphyte diversity differs depending on:

1. the altitude of the study site
2. the host tree,
3. the height within a tree,
4. the number of trees studied.

1. Lowlands were regarded as less rich in species. A comparison of an andine forest in Venezuela and a lowland forest at the Upper Orinoco revealed distinctly less species (León-Vargas 2001).

2. The bark structure and bark chemistry of the host tree has important influence on the number and composition of epiphytic bryophytes. The bark can be smooth, cracked or flaky to various degrees. Smooth bark does not much accumulate humidity or humus and has usually lower numbers of species. Furthermore, this type of bark is often colonized by crustaceous, even endophytic lichens. These lichens have an allelopathic effect on bryophytes and flowering plants and inhibit their colonization. In experiments, aqueous extracts of these lichens inhibited spore germination of bryophytes and well as seed germination of Bromeliaceae (Frahm et al. 2000). This effect has been detected in a tropical lowland rain forest in Venezuela, where

a determination of the cover of epiphytic bryophytes revealed that a high percentage of trees had no bryophyte cover. These trees were trees with smooth bark and covered with crustaceous lichens. Flaky bark is hardly colonized by bryophytes. Important is also the water storing capacity of the bark. Soft bark stores more water and this water is released over a longer time, resulting in more luxuriant epiphyte grows. Another factor is the pH of the bark. This factor is not as important in the tropics, because there are apparently no trees with basic reaction in contrast to temperate regions, where some trees have barks with an pH of around 7. Measurements in different parts of the tropics (Frahm 1987, 1990, 1994) revealed that the pH of bark of tropical trees ranges between 4 and 6. As phytosociological studies have shown, the composition of species depends on differences in the bark pH. This explains that we have different bryophyte communities on tree trunks in the same study area on different trees.

All these factors also concern host trees in the extra tropics.

3. There is an uneven distribution of epiphytes within a tree. The results of such studies, however, differ. Richards (1984) studied 28 cut down trees in a lowland rain forest in Guyana. He found that the understorey is richer in species and the canopy has less species due to harsh conditions of high light intensity, strong desiccation and high temperatures. In contrast, a study of also 28 trees in French Guiana using climbing techniques revealed an increase of mosses, liverworts and lichens above 5 meters (Montfort & Ek 1990). Therefore Gradstein called it a myth that lowland forests are poor in bryophyte species since their species richness is located in the canopy (where the bryophytes have more light). A similar effect could be observed in a montane forest in Ecuador (Müller & Frahm 1998), where only 14 of a total of 67 bryophyte species were found on the trunks of 10 trees. Also in a montane forest in Venezuela, the canopy had higher species numbers than the trunks (León-Vargas 2001). Especially the number of mosses in the canopy is higher, because they are more drought tolerant.

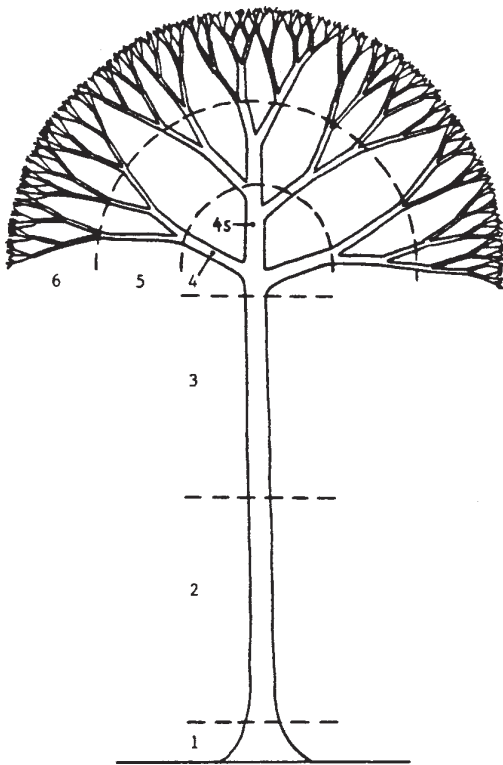


Fig. 5.1: Epiphyte zones after Johannson (1974).

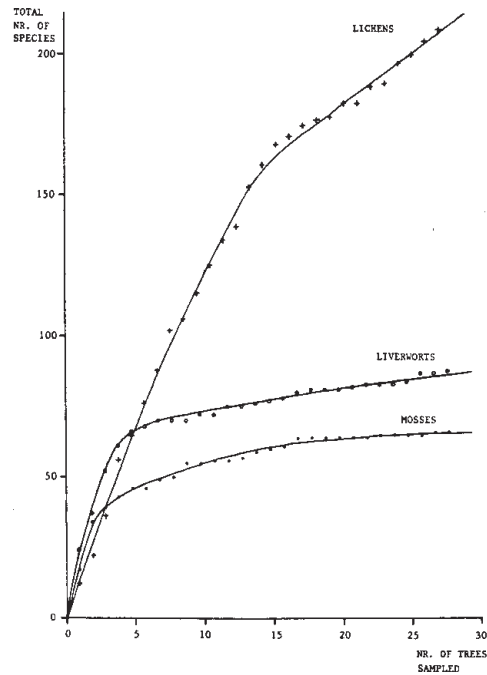


Fig. 5.2: Species per tree number curve (from Montfort & Ek 1990)

4. Also the number of trees studied is important. A „minimum tree curve“ (fig. 5.2.) can give an estimate. In this case, a minimum of 5 trees per study plot is required for a representative inventory.

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Fig. 5.3: Crane above the rain forest canopy of a lowland rain forest, Surumoni-project, Upper Orinoco.



Fig. 5.4: Bryological studies in the gondola of the crane in the canopy, Surumoni-project.

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5.1.2 Epiphylls

The study of epiphylls has gained much attention since epiphylls are said to be a special characteristic of tropical rainforests, although they are more a characteristic of all evergreen rainforests and occur also in temperate rain forests (e.g. the Valdivian rain forest, where is probably the origin of this life syndrome). Epiphyllous growth requires high rainfall and the presence of suitable leaves. Primarily, the leaves function for bryophytes simply as substrate which is shown by the fact that bryophytes can also grow on lizards, turtles, beetles or coke bottles. Even filmy ferns can be colonized as well as other bryophytes. Only some bryophytes are substrate specific, many epiphyllous species can be found on other substrates as well. The degree of epiphyllism increase with humidity and the higher the humidity the more corticolous bryophytes shift from bark to leaves.

The habitat is shared with lichens, fungi, green algae and cyanobacteria. It forms a special environment called „phyllosphere“. Conspicuously, most epiphylls are hepatics of the

family Lejeuneaceae, which counts for 95% of all epiphylls, which have especially adapted to this kind of habitat. The **morphological adaptations** include:

- short life cycle
- reduction of the gametophyte (neoteny)
- diaspore production after a short time
- frequent production of gemmae
- adaptation for fixation on the leaf by mucilage secreted by plants or gemmae, development of rhizoid plates.

Diversity studies (e.g. Lücking 1995, 1997) include the analysis of diversity on single leaves, single localities and larger geographical areas.

Ecology studies include the determination of the influence of altitude, leaf preferences, composition of species, micro climate, and human influence. Few species are confined to the lowlands; most species occur from the lowlands to 1600, from the lowlands to 3000 m or between 500 and 1600, 500 and 3000 or 1600 and 3000 m (Eggers 2001). The increase with the elevation is caused by increasing facultative epiphyllous species. A decrease of diversity is caused by dry climate and human influence, resulting in covers of small, closely appressed species, whereas in strongly humid conditions, the epiphyllous species can even change to upright growth. Three microsites can be differentiated: shady understorey, light gaps and the canopy. The most species rich sites are light gaps with sufficient humidity, especially sites along streams. Another topic of interest are **interactions** with other foliicolous organisms and the host leaf. Epiphylls absorb light intensity. Especially in shady habitats with less than 2% relative light intensity and in leaves with a high cover of epiphylls, this effect can harm the host plant. On the other hand, epiphyllous bryophytes with their antifeedant effects might deter leaf herbivores including leaf cutter ants. An important interaction is that with cyanobacteria, which live in close contact with bryophytes which provide a humid micro-environment for them. The nitrogen fixed by the cyanobacteria can be taken up by the epiphyllous bryophytes as well as the host leaf (Bentley & Carpenter 1980, 1984, Bentley 1987, 1989, Carpenter 1992). Competition, e.g. with epiphyllous lichens, has not yet been studied much. It may not be so important, since both seem

to have avoidance strategies.

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Fig. 5.5: Epiphyllous bryophytes in a Ecuadorian lowland forest (Rio Palenque).

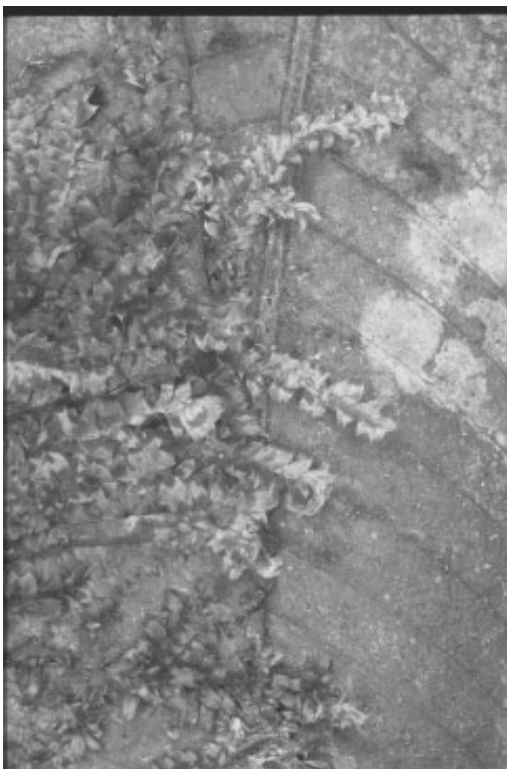


Fig. 5.6: The moss *Crossomitrium* spec. growing on a leaf (Colombia Dépt. Chocó).

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5.1.3 Rotten wood

There is little information on bryophytes from rotten wood, which is one of the few habitats for bryophytes in lowland forests. This habitats is usually occupied by Sematophyllaceae, Hookeriaceae and Leucobryaceae. In montane forests, the bryophyte flora on rotten wood is richer since the trunks are not so fast decayed. In Tanzania, 102 species of bryophytes were identified from rotten woods (Mattila & Koponen 1999). The bryophyte vegetation varies depending on the stage of decomposition. An easy method to determine this stage is the determination of the depth of penetration of a knife (e.g. 1: knife does not penetrate, 2. penetrates one centimeter, 3, penetrates several centimeters, 4. penetrates to the handle).

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5.1.4. Tree Ferns

Tree ferns are an ideal substrate for bryophytes, causing a rich vegetation. They have, however, gained no special interest in the past. The first and only study was performed in SE-Brazil on *Cyathea* and *Dicksonia* trunks. A total of 142 species was found on these trunks. Most species grew only by chance in this habitat, only 20 of the species was found in more than 10% of the tree fern trunks studied. Five bryophyte associations could be described, of which three

were found on *Cyathea*, two on *Dicksonia* trunks. Tree ferns are very ancient plants; they existed already in the Mesozoic and provided a constant microhabitat for more than 100 mio years. Therefore the relation between the bryophyte vegetation on tree fern trunks in SE-Brazil and in New Zealand was studied. The associations in both parts were not just composed by identical species but by vicariant species. For instance, *Hymenodon aeruginosus* in New Zealand is replaced in Brazil by *H. pilifer*, *Pyrrhobryum bifarium* by *P. spiniforme*, *Hypopterygium didictyon* by *H. tamarisci*. This shows that in different parts of the world species of the same genus compose associations on comparable habitats, due to their common habitat preferences.

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5.1.5. Unusual substrates

The higher the humidity, the lower is the influence of the substrate. If there is sufficient atmospheric supply with water and nutrients, bryophytes (and especially also lichens) can grow on any substrate, including shells of water turtles, old shoes, traffic signs of old cars. Therefore it is not surprising that bryophytes from tropical forests can also grow epizoic on beetles and lizards.

Another unusual substrate has been reported from Peru (Frahm 1985) and was also observed in Venezuela: bryophytes growing on ant gardens in the canopy (fig. 5.7).

- Frahm, J.-P. 1985.** A Bryophyte in an Ant Garden. *Bryol. Times* 34:1.
- Gradstein, S. R., and C. Equihua. 1995.** An epizoic bryophyte and algae growing on the lizard *Corythophanes cristatus* in a Mexican rain forest. *Biotropica* 27:265-268.
- Gradstein, S. R., D. H. Vitt, and R. S. Anderson. 1984.** The epizoic



Fig. 5.7: The moss (*Brachymenium columbicum*) growing in an ant garden (NE-Peru)

occurrence of *Daltonia angustifolia* (Musci) in Papua New Guinea. *Cryptogamie, Bryologie et Lichénologie* 5:47-50.

Gressit, J.L., Samuelson, G.A. & Vitt, D.H. 1968. Moss growing on living Papuan moss-forest weevils. *Nature* (London) 217: 765-767.

ve than vascular plants and have the advantage, that they are much less numerous. Whereas it makes enormous difficulties to determine the vascular flora along an altitudinal transect, the determination of bryophytes is much easier. This could be proved all around the world, in Peru, Colombia, Central Africa and East Asia.

There are several different attempts to determine the altitudinal zonation of rain forests:

- by floristic analysis

For that purpose, the species composition is determined along a transect. It is sufficient to focus the analysis on representative (undisturbed) areas. Intervals of 200 m altitude are sufficient. As a representative area, one hectare has proved useful, since such an area is most widely used and allows comparisons, however, also 25 x 25 m can be sufficient depending on the structure of the forest. All species are noted, collected and identified and arranged in a table. It can be seen from such a table that certain species cluster together. These species are grouped together and allow a vertical classification. The composition of species or the restriction of certain genera to

5.2. Altitudinal zonation

5.2.1 Determination of altitudinal belts

As figured out in chapter 4, bryophytes are adapted to different ecological conditions by morphological and anatomical structures. These adaptations vary according to the environment. Since the environmental conditions vary with the altitude, we found differently adapted bryophytes in different altitudes. Therefore bryophytes are a useful tool for elaboration of altitudinal zonations. Bryophytes react much more sensi-

vertain altitudes is so characteristic in tropical forests, that a bryologist with some experience can often determine the altitude as exact as 200 m without altimeter by bryophytes only, since many species and genera are indicator species for certain altitudinal belts. The absolute elevation is only modified by the humidity: the higher the humidity the more are the altitudinal belts depressed. In hyperhygric conditions, the species characteristic of higher altitudes go far more lower down than in drier regions..

- by species numbers

Beside the species composition, also the number of species per area is significant for different altitudes and shows a characteristic curve along a transect. Therefore it is not necessary to identify all species but to determine the number per area (fig. 5.8). Species numbers in the forest understory are comparably low in the lowland forest, increase a bit in the submontane forest, show another increase in the lower montane forest and a highly significant increase in the upper montane forest and a decrease at and above the forest line.

- by determination of floristic discontinuities

A variation of the both previous method is the following: all species have lower and upper ends of their ranges along a transect. Therefore it is determined from the table showing the occurrences of the single species in the relevés along a transect, how many species have their uppermost viz. lowermost occurrence in every altitude. The results are plotted in a graph (fig. 5.9). The altitude, in which a maximum number of species with lower- or uppermost occurrences is found, indicates a shift in the species composition, and thus a change in the zonation.

- by estimation of cover

Also the determination of the cover of bryophytes either on soil and rocks or on trees gives an clear altitudinal zonation (cf. fig. 5.10). Reason is that the amount of phytomass is determined by physiological factors, which change along a transect (see chapter 5.3) and phytomass is an expression of these changing ecological conditions.

- by determination of life form spectra

Autecological adaptations reflect changing environmental conditions, too, as explained in chapter 4. By this way, useful altitudinal zonation can be derived even without any determination of species.

- by estimation of phytomass

Similarly to the estimation of cover, the determination of the phytomass of (preferably epiphytic bryophytes) give valuable result for constructing altitudinal zonation (see also chapter 5.3).

In total, all methods described here give identical results.

5.2.2 Results

There are numerous classifications and terminologies characterizing the altitudinal belts in the wet tropics. They were differently derived from the aspect of the forest (height, presence of palms, tree ferns etc.), which was commonly used by geographers, or by various groups of animals including butterflies and birds. The belts are differently named with local names (tierra caliente, tierra templada, tierra fria or selva neotropical inferior, bosque subandino or bosque andino), as rain forest, montane forest, cloud forest, mist forest, or with numbers. The terminology, however, should be worldwide comparable and thus use the same system. A classification into lowland, submontane, lower montane, upper montane and subalpine forest is therefore recommended. For indication of the tropical conditions, the prefix tropical should be added.

The altitudinal zonation derived from bryophytes is primarily a climatic one: climate factors determine the species number, species composition, adaptation and phytomass. It is therefore not a classification for bryophytes but for the ecological conditions of the forest.

In equatorial latitudes, the altitudinal belts are as follows:

- 3-400 m: tropical lowland forest
- 1100-1300 m: submontane forest

- 1800 m: lower montane forest
- 2800 m: upper montane forest
- forest line: subalpine forest

The limits of the altitudinal belts vary moderately. They depend on:

- the elevation of the mountain. Low mountains have the altitudinal zonation compressed and a distinct peak effect at top, causing subalpine conditions even at lower altitudes. Higher mountains have the altitudinal belts extended. This is explained by higher temperatures, caused by the „mass effect“ of the mountain.

- isolated mountains differ from mountain ranges
- the exposition. As everywhere in the world, N-exposed slopes have lower limits than S-exposed slopes. This is a strong indication that the zonation is also caused by the temperature.

- the humidity. Regions with higher precipitation have depressed altitudinal belts. The reason is amongst other factors that the temperatures are lowered. Another reason is, that the high humidity, which is found e.g. in the high montane belt, and which is dependend for certain bryophytes, is realized already at lower altitudes.

- the latitude. The forest line is declining from the equator towards the poles, until it reaches sea level in the arctic/antarctic. By this way, the altitudinal belts are not compressed but they and at sea level depending on the latitude following the model by Troll (fig. 5.7). This means that for instance in SE-Brazil, we have no lowland forest but the forest starts with an submontane forest at sea level. This forest in SE-Brazil has the same „mossiness“ and comparable phytomass, cover and species numbers as a tropical forest in 800 m in equatorial latitude. In Patagonia, the subalpine forest ands at sea level. In fact, the bryological characteristics of the forest in Patagonia and in Ecuador at 3300 m are very similar, and even many species are found in both forests.

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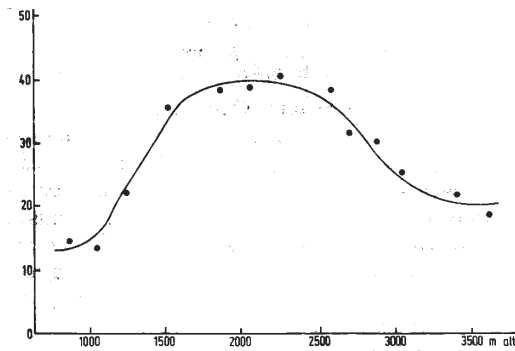


Fig. 5.8: Characteristic species curve along a transect in Colombia between 950 and 3500 m (after Van Reenen & Gradstein 1983).

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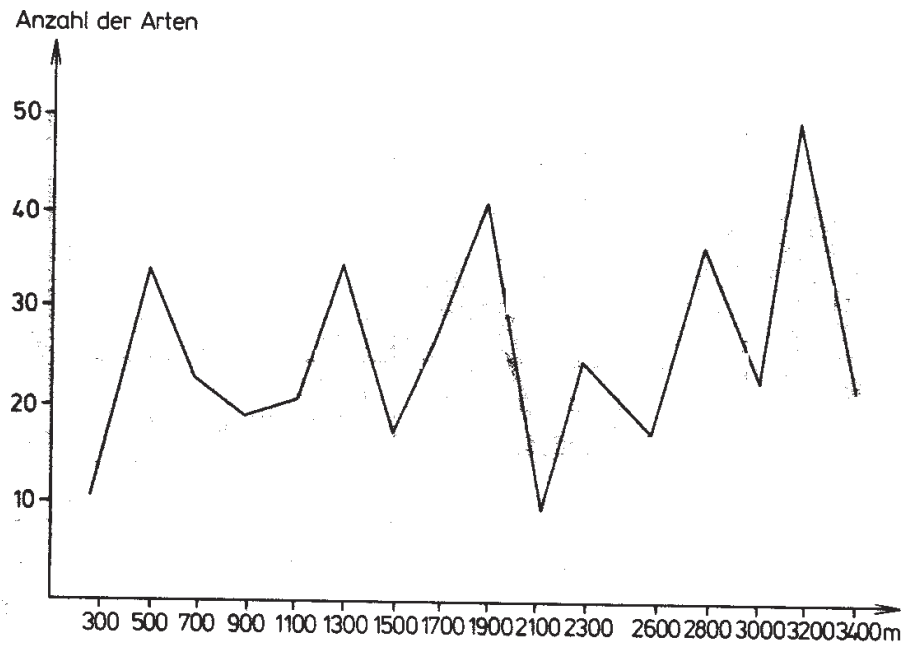


Fig. 5.9: Determination of the floristic continuities along a transect from the lowland rain forest to the forest line in NE-Peru (after Gradstein & Frahm 1987). The peaks indicate elevations, in which most species have either their upper- or lowermost occurrence thus indicating a floristic change.

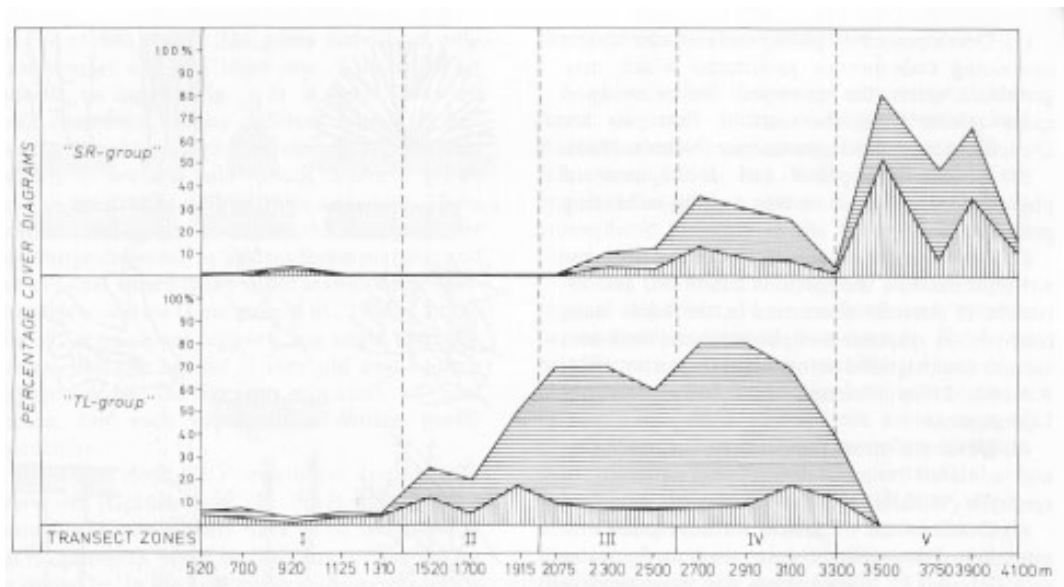


Fig. 5.10: Bryophyte cover values along a transect in Colombia (after Van Reenen & Gradstein 1983). I: lowland forest, II: submontane rain forest, III: lower montane rain forest, IV: upper montane rain forest, V: paramo. SR group: terrestrial and saxicolous species, TL-group: epiphytes.

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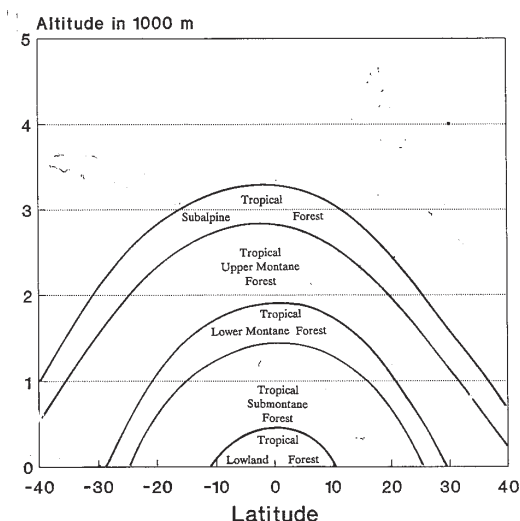


Fig. 5.7: Scheme of the altitudinal zonation between 40° S and N (after Troll).

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5.3 Phytomass and water storage capacity

(with collaboration by T. Pócs)

An important ecological rôle of bryophytes in tropical rain forest areas is the water storage function. By this way, bryophytes

- regulate the level of water courses
- prevent soil erosion
- warrants water supply for a much larger area for
 - drinking water
 - irrigation
 - energy.

Beside, deforestation has the effects of

- seasonality of watercourses (desiccation and inundation)
- drying and warming up the local climate
- topsoil erosion (up to 4 cm per year)
- torrential rains causing landslides.

Therefore catchment forests are required in montane areas. To determine the rôle of bryophytes, studies of the water storing capacity of epiphytic bryophytes have been undertaken in several parts of the tropics. The results are difficult to compare, since some authors determined the phytomass of single trees, others per square meter, and accordingly estimations of phytomass per hectare vary. On horizontal branches, humus accumulated below the bryophytes may be included in the calculation or removed before measurement. The same concerns the determination of the water storage capacity. Part of the water is stored by the plants, another part is stored between the plant (interception water). The storage capacity of bryophytes is usually three times of the dry weight. A higher percentage of Leucobryaceae and Calymperaceae with specialized water storing adaptations can raise the value to 5 times. Interception water is difficult to determine since it easily runs off when the bryophytes are balanced. In any case, these studies give an idea of the relations.

Jacobsen (1978) was the first who made phytomass measurements of epiphytic bryophytes in Transvaal. He found 34 g/m² and 34 kg/ha. Pócs (1976, 1980) was the first who determined phytomass and water storage capacity of epiphytes in the Uluguru Mtns., Tanzania. He found 2130 kg phytomass/ha at 1415 m and 10.000 kg/ha phytomass at 2100 m elevation. The water storage capacity was 15.000 viz. 50.000 l/ha. Of the 10.000 kg total phytomass, 8.000 kg were found in the canopy. In the Nguru Mtns, Tanzania, Björk & Mareby (1992) found 13.000 kg/ha with 53.000 l water storage. Wolf (1993) determined 2000 kg phytomass/ha with 10.000 l water storage in an Andean forest in Colombia at 1500 m elevation and 20-23.000 kg/ha with 80-1000.000 l at 3500 m.

Additional calculations of phytomass and water storage capacity was made Frahm (1987) in Peru, Frahm (1990) in Borneo, Hofstede et al. (1993)

in Colombia and Frahm (1994) in Zaire. A survey (at the former state of knowledge) of bryophyte phytomass in tropical ecosystems was given by Frahm (1990).

In a less mossy forest at Mt. Kilimanjaro, Pócs (unpubl.) determined a water storage capacity of 4500 l/ha in an intact forest but only 2700 l/ha after logging.

Phytomass increases with elevation (see chapter on altitudinal zonation). A considerable amount of epiphytic phytomass is reached above 2000 m, which stresses the importance of high montane forests. Below 1000 m, the epiphytic bryomass is with 10-12 g/m² quite low in all tropical regions studied (Frahm 1987, 1990, 1994). Maxima are realized at the forest lines. There, the phytomass can be 1000 times as high as in the lowland forest. Reason are high temperatures and low light intensities at lower altitudes (see chapter ecophysiology). Local microclimatic conditions (cloud belts, „elfin forests“ at mountain ridges) can have a strong influence on these values.

The highest phytomass is found on branches, especially horizontal branches, and not on the trunks of trees. Accordingly, the water storage capacity of branch epiphytes is higher (Björk & Mareby 1992). Naturally, the larger the tree the higher the water storage capacity, which emphasizes the value of old growth forests.

Although the values for water storage capacity are impressive, the following points have to be considered (Frahm 1994):

- in rain forest climates, the bryophytes are rarely really dry and cannot take up the full amount of water. During rain fall, the bryophytes are soaked very fast with water and the additional rain water cannot be stored. To eliminate this effect from the calculations of water storage, the interception water can be neglected.

- the percentage of the total rain fall stored by bryophytes is very low. In an area with 4000 mm of annual rain fall, we have a precipitation of 40 million liters per hectare and year. Assumed it is raining every day, we have 109.589 l/ha rainfall per day. If the water storing capacity of bryophytes is 10.000 l/ha, only 10% of the rain fall is stored by bryophytes, presumed that the bryophytes were totally dry before rainfall (what they not are). At lower altitudes with accordingly lower rates of phytomass, the percentage of rain

stored by bryophytes gets much lower to rates of 1-2% of the precipitation and is at least even negligible in lowland forests.

The effects of phytomass and water storage capacity are not confined to tropical forests but similar in other types of humid forests such as temperate rain forests or montane forests in temperate regions. They are simply related with the humidity, which is increasing with elevation in almost all mountains.

Most of the retained water presumably evaporates, contributing to a high air humidity, condensation of clouds and again to rainfall. Bryophytes have therefore importance for a balance of the climate and avoid drying and warming of a landscape.

Beside of the phytomass of epiphytic bryophytes, also the **terrestrial bryophytes** play an important rôle for water storage. This especially concerns subalpine forests, where the ground is densely covered with bryophytes. So far, no studies of the water storage capacity of bryophytes in have been performed in the tropics. It can be assumed that these bryophytes contribute at least the same amount if not more to the water storage. The ecological function of the bryophytes on the ground is that they store water to a certain amount and evaporate it to the atmosphere. If the bryophytes are saturated with water, additional water does not run off causing erosion but feeds the ground water.

A much neglected effect of epiphytic bryophytes is the **uptake of nutrients**. Rain water is the source of nutrients for all epiphytic and most epigeic bryophytes. If rain water would run off, also the nutrients would run off. If it is taken up by bryophytes, the nutrients are incorporated to built up organic phytomass. If this phytomass is later decomposed, the nutrients are incorporated in the ecosystem. This effect concerns especially epiphytic „moss balls“, which can grow to enormous size and weight, and break down from canopy branches when they got too heavy. According to Veneklas (1982), the humus produced by rotten epiphytes is in average 10% of the epiphytic phytomass (it varies between 2 and 65%). This humus can be 2500 kg/ha (Pócs 1976, 1980).

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5.4 Human impact

Bryophytes are a very valuable tool for measuring disturbance of habitats. This concerns especially the recognition of primary forests and its differentiation from secondary forests for two reasons:

1. Secondary forests have a different structure and micro climate. The more open structure favours sun epiphytes and reduces shade epiphytes. Species of secondary forests are more drought resistant and have a broader ecological

amplitude for light and humidity. Even selective cutting of trees results in changing humidity conditions and changing bryophyte composition. Florschütz-de Waard & Bekker (1987) observed in the Guianas that the epiphytic species in the plantations were the same as in scrubby vegetation around. These species were again the same as those from the rain forest canopy. A small tree near the ground in the open is ecologically comparable to the canopy in 25 m elevation and both are colonized by sun epiphytes. Hyvönen et al. (1987) stated that the species confined to primary rain forests in Papua New Guinea are shade epiphytes

2. Species of secondary and primary forests have different reproduction strategies. The species of primary forests have facilities to propagate vegetatively and can survive in sterile conditions. In terms of life strategies, they are stayers. After a clear cut, the regrowth has to be colonized from larger distance. In terms of life strategies, these are colonists. The recolonisation of the secondary forest has to start from zero with different species.

Therefore secondary forests have a very different epiphytic bryophyte flora. Pócs (1982) observed that 90% of the species of native forests did not occur in plantations. Nevertheless, secondary forests may have a higher diversity than primary forests, at least with regard to trunk epiphytes. Epiphytic bryophytes can be very abundant in coffee, citrus, mango, rubber or cocoa plantations to such an extent that they must be removed. Therefore species numbers alone does not tell too much, the indicator value of the species must be considered. The quantity of species is not sufficient but the quality.

Similarly, foliicolous bryophytes can be sensitive for disturbance. However, except for human made disturbances, there are also natural disturbance effects such as the effects of El Niño on the cryptogamic vegetation of Galapagos, the effects of hurricanes in the West Indies, those of volcanic eruptions including the effects of soil ashes and plants and the forest floor, climatic fluctuations, especially wetter and drier periods.

Equihua, C. & S. R. Gradstein 1995 .

Hofstede et al. (1993)	Kolumbien 3700 m	?	44000
Pócs (1976)	Tanzania 1415 m	63	1773
	Tanzania 2120m	?	10300
Jacobsen (1978)	Transvaal	34	340
Frahm (1987)	Peru 3200m	140	?
Frahm (1990)	Borneo	400	1320
Frahm (1994)	Zaire 3200m	600	6000

Tab. 5.1: Phytomass of epiphytic bryophytes in kg/m² and kg/ha in different regions of the tropics.

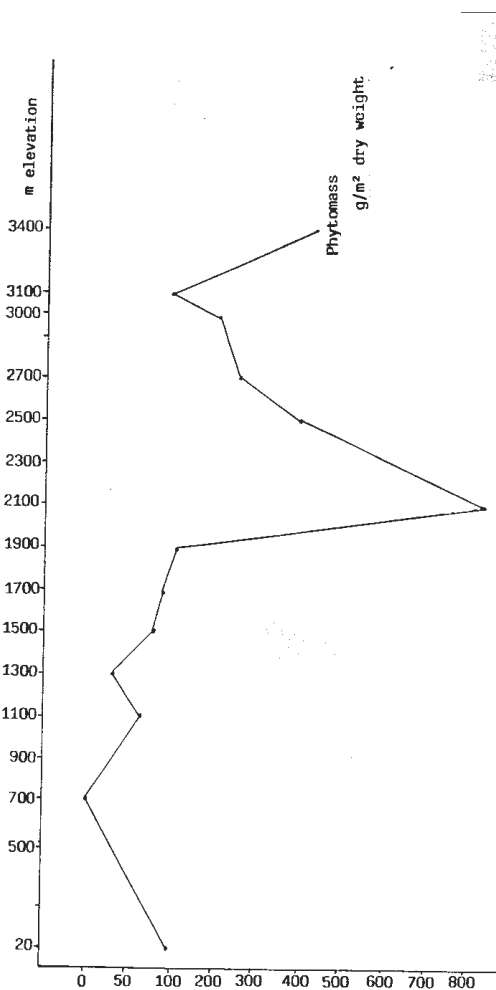


Fig. 5.8: Phytomass of epiphytic bryophytes per hectare along a transect on Mt. Kinabalu, Borneo. The low values around 2700 m are caused by a forest type on ultrabasic soil. The higher values at 20 m are caused by the nearby coast.

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6 ECOPHYSIOLOGY

The ecophysiology of tropical bryophytes is still a much neglected field, because only few physiologists have studied bryophytes in the tropics and the classical bryologists usually did no physiological work. Furthermore, the working conditions for physiologists in the tropics are not the best. An understanding of the ecological behaviour of bryophytes can, however, only be reached if their physiology is known.

6.1. Temperature, light and humidity

A conspicuous effect of the bryophyte vegetation in the tropics is the increase of „mossiness“ with the altitude. This effect has fascinated even botanists in the 19. century. Several attempts have been made to explain this effect. Increasing precipitation or humidity with the altitude was argued, although the precipitation in the lowlands can already be quite high, decreasing temperatures were also introduced as argument, more light intensity at higher elevations, desiccation in the lowlands, but all arguments could not explain this effect satisfactorily because they were gaps in the argumentation or exceptions. During the BRYOTROP expedition in Peru, attempts were made to clarify this problem with ecological measurements. There were in fact good correlations between the

phytomass of bryophytes on the one hand and the light, temperature, and humidity. However, it could not be explained why bryophytes did not occur in the lowlands e.g. along road cuttings where they get as much light or more as at higher altitudes. The key to solve this problem was a combination of factors as suggested already by Richards (1984). Richards regarded a combination of temperature and light intensity as important, when he wrote: „Studies of photosynthesis, respiration and net assimilation rates in lowland and montane forest bryophytes might be of great interest in this connection“. Therefore first laboratory experiments were performed (Frahm 1987, 1990) to test this hypothesis. Tropical montane bryophytes were kept in a climate chamber and treated under lowland conditions (high temperature of 30°, low light intensity of 300 Lux) and montane conditions (10° and 1500Lux). The result was, that bryophytes did not gain net photosynthesis under lowland conditions because of high respiration. The respiration during night time was higher than the photosynthesis over day, resulting in a negative net-photosynthesis. Similar results were obtained by Löscher et al. (1994) with material collected in Zaire. Zotz et al. (1997) and Zotz (1999) could support this explanation with field experiments performed in Panama in various altitudes between 30 and 1200 , also for folious

lichens, which have a similar physiology as compared with bryophytes.

The photosynthesis of tropical montane bryophyte species does not differ from those from temperate regions. The physiology nicely supports that these species are phylogenetically derived from temperate species.

It is still an open question how the (fewer) bryophytes in the tropical lowlands can survive under these conditions, which montane species cannot tolerate. One hypothesis is that the low light intensity is compensated by higher carbon dioxide, which originates from rotten plant material close to the ground. This would explain the effect that sometimes epiphylls in lowland forests have a distinct upper limit in about 1 m. Another possibility would be that they have different phytochrome systems to gain more photosynthesis under low light conditions. Species in the outer part of the canopy gain more light and thus have a higher photosynthetic rate. They are, however, exposed to severe drying especially at noon.

Changes of factors within the forest.

Within the forest, there is the well known distinct increase of light from the ground to the canopy (fig. 6.2). There is only 1% of the light intensity at the bottom of lowland forests, which is responsible for the low number of species. With the light intensity in the canopy is almost that of open places. On the other hand, the humidity is declining, being high at the bottom of the forest for all over the day and night and reaching even extreme low values in the canopy at noon (fig. 6.3). Thus the bryophytes at the bottom have to suffer from low light but have high humidity, those in the canopy have to suffer from strong desiccation and high temperatures but have more than sufficient light. Both requires morphological and anatomical adaptations. The critical value of the humidity for bryophytes is 80% rH. This is based on observations in the field, according to which bryophytes dry up below 80% but stay turgid above 80%. Reason is, that bryophytes can take up humidity from the air by their high osmotic values. As poikilohydric plants, bryophytes have metabolism only in wet state, so long as they are turgid. They have photosynthesis only in light phases when

turgid. Dark phases in wet state must be deducted from the balance because they cause respiration. And this is a problem with species in the understorey, which live under conditions of low light intensity over day but strong respiration loss over night. It has so far not yet studied how the bryophytes in the understorey of lowland forest can reach net photosynthesis. One possible explanation could be that they reach higher rates of photosynthesis from light spots shining through the canopy and wandering with the sun over the ground of the forest. This could explain why bryophytes have such a scattered, uneven distribution at the bottom of the forest.

Changes of factors with the elevation.

Within a transect from the lowland to the subalpine forest, the important factors of light, temperature and humidity are changing, which is the reason for the different life form spectra, the different growth forms, and various anatomical adaptations of species as well as the increase of biomass of bryophytes.

The temperature decreases constantly by 0.6°C per 100 m elevation (fig. 6.4). The mean annual temperature can easily be determined in the tropics by measuring by the soil temperature in 30 cm depth.

The light intensity within the forest is increasing with the elevation due to lower forests with smaller leaves (fig. 6.5). This causes an increase of bryophytes in the ground layer from almost zero to almost 100% in the subalpine forest.

It is a myth which is propagated in many ecology textbooks that the tropical rain forest has consistent high humidity. Measurements in many parts of the tropics revealed that there is a decrease of the humidity at noon, which can reach 60% rH or less (fig. 6.6). In fact, we have an increasing air humidity with the elevation because of the decreasing temperatures because the water contents of the air declines with the temperature. Thus the air at high temperatures in the lowlands takes up more humidity than the air at lower temperatures in the mountains, resulting in a decrease of the relative humidity. If the air cools down continuously with the elevation, the saturation point will be reached causing mist or clouds. This is the reason that cloud forests are found only at higher altitudes.

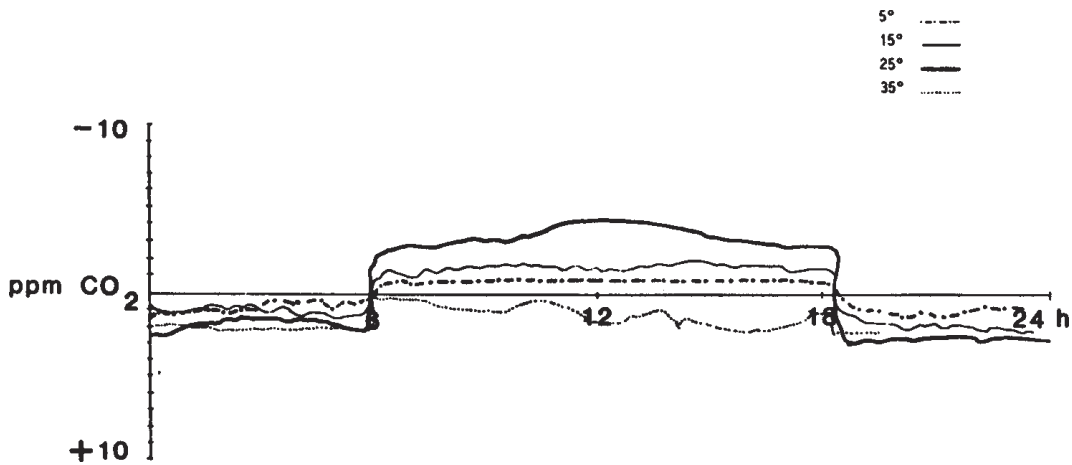


Fig. 6.1: Photosynthesis of *Plagiomnium rhynchophorum* under various temperature conditions at 1500 Lux. The montane forest conditions (5°, 15°) give a sufficient net photosynthesis, the lowland condition (25°) gives photosynthesis over day but no net-photosynthesis. 35° gives no net photosynthesis during day.

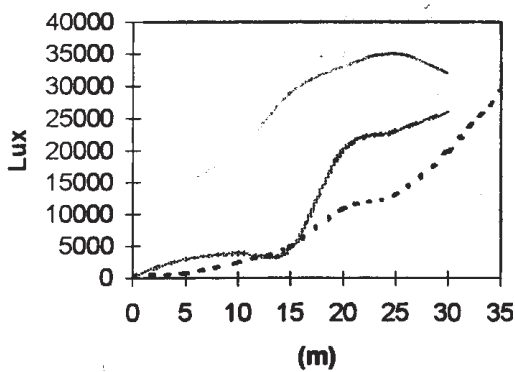


Fig. 6.2: Profile of light intensity in an Amazon lowland forest (Surumoni, upper Orinoco). From León-Vargas 2001.

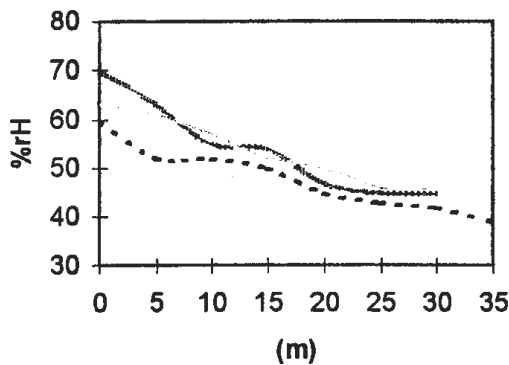


Fig. 6.3: Profile of humidity in an Amazon lowland forest (Surumoni, upper Orinoco). From León-Vargas 2001.

Instructions for performing measurements of ecological factors such as temperature, humidity and light are given in the appendix.

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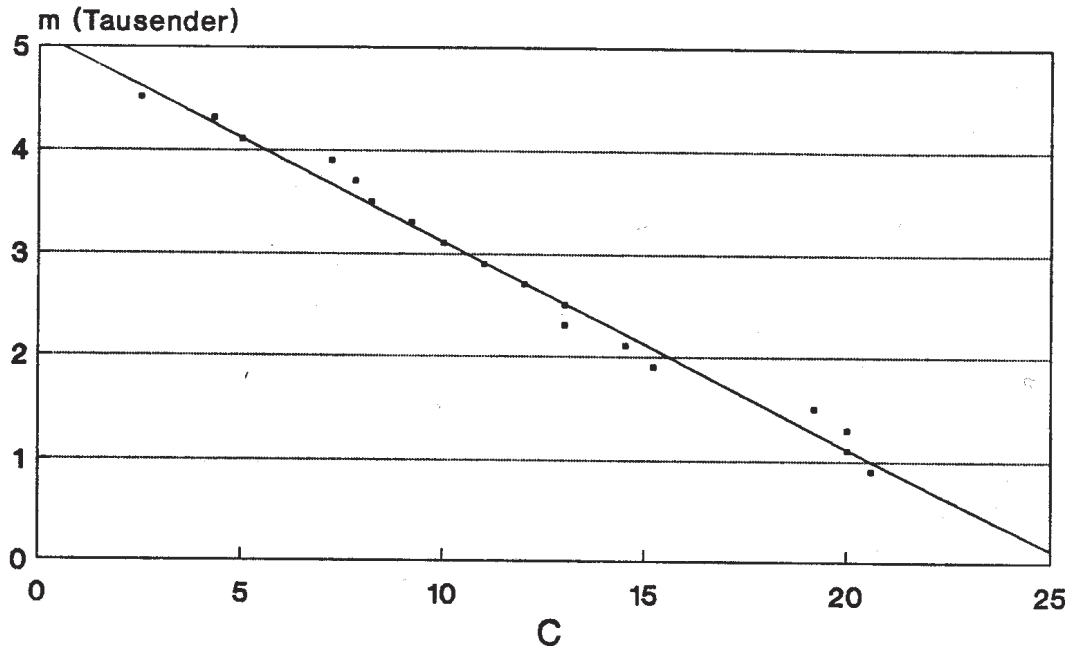


Fig. 6.4: Mean annual temperatures (derived from soil temperature) along an transect in Eastern Congo/Uganda. The decrease is almost constant.

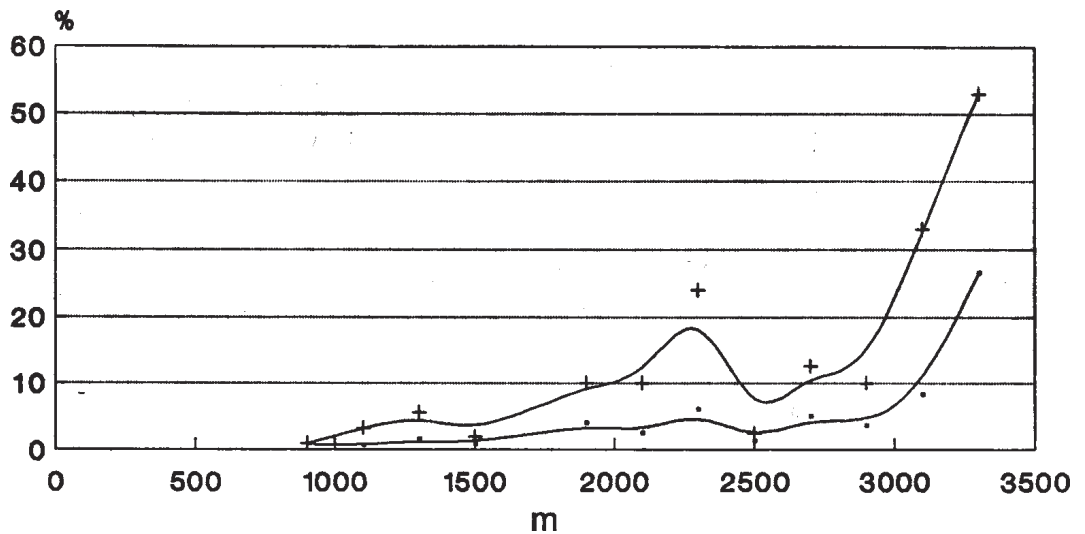


Fig. 6.5: Minima and maxima of relative light intensity in percent (as compared to the situation outside the forest) at the bottom of rain forests in Eastern Congo/Uganda. The light increases slightly from the montane to the high montane forest and reaches maxima in the subalpine forest.

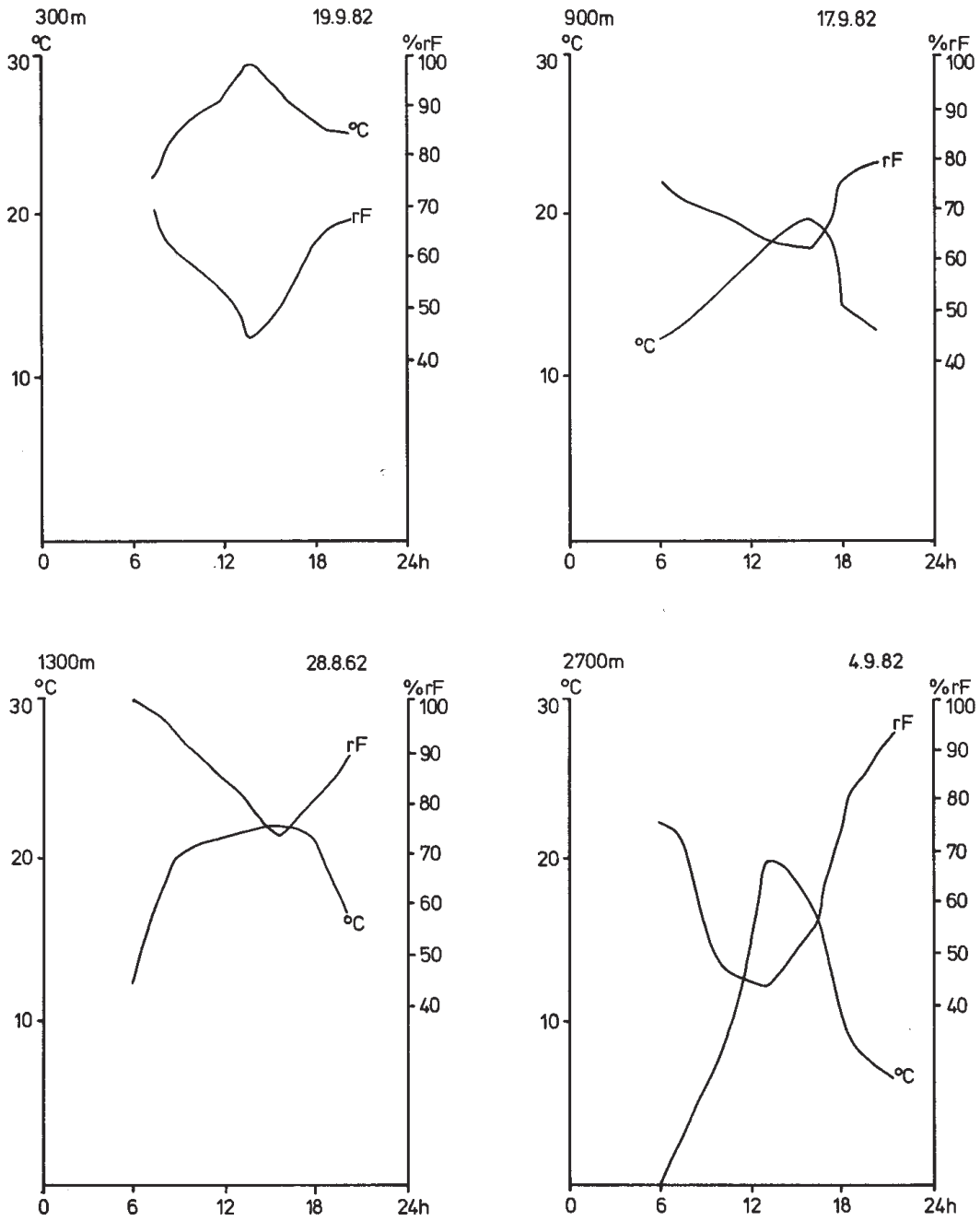


Fig. 6.6: Daily curves of temperature and air humidity in different elevations along a transect at the E-slope of the Andes in NE-Peru. At 300 m, the temperature raises at noon to 30° but the humidity drops down to 45%. With increasing elevation, the temperature decreases causing a higher relative humidity. The overlapping parts of the curves show not saturated air humidity (only short time at noon).

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7. BRYOSOCIOLOGY

Like all other plants, also bryophytes are growing together in distinct compositions of species, which are called associations. These are composed of species with similar habitat preferences. The species composition is very regular and typical. The name of an association implies a combination of numerous species and allows to characterize certain habitats, altitudes and climatic conditions. As species can be grouped by similarity to genera, families and orders, also associations can be grouped in a hierarchical system.

This field called plant sociology has been developed in Europe and applied mainly in Europe, later also in comparable regions (Japan). In North America, different techniques in the way of vegetation analysis and statistics is used instead. They have no standard methods for the field, for table work and for evaluation have no classification and therefore do not allow to compare plant communities from different regions.

For a long time it was supposed that the European plant sociology technique can not successfully be applied in the tropics. This may still concern certain types of rain forests with a high diversity of trees. First attempts in the páramo vegetation of Colombia (Cleef 1981) and later studies by Mrs and Mr Miehe (plant geographers from the university of Marburg, Germany) in tropical African mountains revealed that these methods can be used in the tropics quite well with the result that vegetation units can be typified and classified.

Bryophyte associations have also been described mainly from Europe, rarely also from Japan, and only few attempts were made to describe bryophyte associations in the tropics (Akande & Olanmoye 1982, Augier 1972, 1974, Giacomini & Cifferi 1950). In part, these „associations“ or „communities“ were not described in a phytosociological way (Griffin 1974, Jovet-Ast 1949, Miller 1954). Even for the German BRYOTROP project, first approaches to determine the epiphytic bryophyte vegetation in Peru included only descriptive and statistical methods (Frahm 1987). (The tree trunks were wrapped with plastic, the patterns of bryophyte species was copied with colour ink pens on the plastic, the cover was calculated and the affinities between the species calculated by Chi-Square tests). Later, the work of Kürschner (1990a, 1990b, 1995a, 1995b) in Borneo and Zaire revealed that distinct epiphytic bryophyte associations can be distinguished also in the tropics, which are characteristic for different altitudes. Therefore Kürschner & Parolly (1998) completed the analysis of tropical epiphyte studies in Peru and could (Kürschner & Parolly 1999) show that worldwide in the tropics there is a system of comparable epiphytic bryophyte communities. This is based on the fact that species of the same genera, in some cases even the same species, are growing in comparable elevations in the tropics, forming vicariant communities (Kürschner & Parolly 1998, 1999). Although this methods was either ignored or heavily criticized

by North American botanists, it has proved to be very successful and useful. Meanwhile, it has also successfully been used to determine bryophyte communities on tree fern trunks in SE-Brazil (Ahmed 2002) and also been used very successfully in temperate rain forests in New Zealand and Chile.

The importance of phytosociology is based on the fact that plant species cannot be seen isolated. They grow - determined by ecological factors - together with other species and even animals (in biocoenoses). Therefore changes of ecological parameters (altitude, disturbance) affect not single species but associations. Furthermore, the name of an association represents and symbolizes a complex of species with all its determining ecological factors and characterizes a certain habitat.

To promote this method in the tropics, a short instruction of the field technique is given in the appendix.

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- Kürschner, H. 1995a.** Epiphytic moss associations in the Eastern Congo basin and the adjoining highlands (National Park Kahuzi-Biega/Zaire, Nyungwe Forest/ Rwanda): Scientific results of the BRYOTROP-expedition to Zaire and Rwanda. No. 4. *Nova Hedwigia* 61:1-64.
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MONTE ZERPA

No.	A10	A1	A2	A3	A7	A9	A4	A5	A8	A6
Altura m.	17	17	18	15	18	19	17	19	22	15
Diámetro cm.	50	38	51	30	38	50	28	60	75	24
Exposición		S-E	N-E	N	W		N-W		W	S-O
Inclinación	87	90	10	50	90	65	2 a 3	15	0	17
Espesor	1,5	5	0,4	1,5	5	1	0,1 a 3	0,2 a 1	1	1,5
Tamaño	40x40	40x40	40x40	40x40	40x40	40x40	40x40	40x40	40x40	40x40
Cobertura tot.		93	92,5						99,5	99

No. total esp.											
Prionodon densus	6	1,5	0,5	0,5	1			{r}		6	IV
Plagiochila A	15	20				12			6	4	III
Taxilejeunea C	60	5		5,5	3	10					III
Liquen A		3,5	1	1		1				0,25	1 III
Radula cf. ramulina		58	0,5		5	3	2				III
Pterobryon densum		1,5			0,5	r					II
Taxilejeunea X	5			6,5	8						II
Plagiochila Y	1					5					15,5 II
Papillaria imponderosa		2				1	r				II
Zelometeorium recurvifolium		r	r				5			0,5	II
Plagiochila V			9	70,5	80					11	II
Thuidium peruvianum		r				30	55				77 II
Leucobryum subobtusifolium vel aff.						r	1	1	2		II
Cyclolejeunea sp.							16				I
Syrrophodon prolifer var. scaber							1,5				I
Leucoloma cruegerianum							0,5				I
Plagiochila T								3			I
Radula sp.								80			0,5 I
Plagiochila U								r			I
Porotrichum expansum	0,5					2				1,5	II
Lejeunea sp.		2	0,5								I
Bryopteris filicina		{1}									I
Porotrichodendron sp.			1								I
Pyrenula sp.			74,8								I
Taxilejeunea cf. pallens			5								I
Metzgeria leptoneura											0,35 I
Phyllogonium fulgens											1,5 I
Lophocolea sp.											0,25 I
Hypopterygium tamariscinum						r					I
Liquen crustaceo									57,75		I
Pilotrichela sp.										1	I
Leiomela bartramioides								r			I
Omphalanthus sp.								r			I
Metzgeria decipiens					0,5						I
Lophocolea coadunata					1						I
Aphanolejeunea verrucosa					r						I
Neckera scabridens	r										I
Liquen B						1			1		I

Fig. 7.1: Plant sociological table composed from different vegetation analyses in a montane rainforest in Venezuela (Monte Zerpa, Mérida). The data were elaborated by students during a course on tropical bryology. The table shows that the epiphytic bryophyte vegetation in this forest can be attributed to one association with several constant species as well as two subassociations reflecting different host trees.

epiphytic bryophyte communities on the eastern slope of the Andes and in Amazonian lowlands of Peru. *Nova Hedwigia* 66:1-87.

- Kürschner, H., and G. Parolly. 1998.** Syntaxonomy of trunk-epiphytic bryophyte communities of tropical rain forests: A first pantropical approach. *Phytocoenologia* 28:357-425.
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- Wolf, J. H. D. 1989.** Comunidades epífitas en un transecto altitudinal en la Cordillera Central, Colombia: datos iniciales sobre la cantidad de especies de briófitas y líquenes. *In* van der Hammen, T., S. Diaz-Piedrahita, and. Alvarez (eds.). *Studies on Tropical Andean Ecosystems*, 3, pp. 455-459. J. Cramer, Vaduz.
- Wolf, J. H. D. 1993.** Epiphyte communities of

tropical montane rainforest in the northern Andes I. Lower montane communities. *Phytocoenologia* 22:1-52.

8. BRYOGEOGRAPHY

Each phytogeographical analysis must be insufficient at present due to insufficient botanical exploration. It has to be considered that botanical exploration in the last century was almost confined to the surroundings of cities, later along roads, and they were usually not carried out systematically. At present it is confined to the availability of roads, however, even such a large area as the Chocó in western Colombia is accessed by only two roads. There are so far no systematical explorations in the tropics such as the grid mappings in Europe, not even on the basis of the UTM grid (50x50 km).

Another problem is the lack of monographs and revisions and the high numbers of taxonomic synonyms. The knowledge about the bryofloras of the tropics has been greatly increasing over the last decades. This can be exemplified by the species of mosses which were known from Peru in different years:

1951: 345

1975: 568

1985: 834

1987: 903

1992: 889 (Menzel 1992)

The recent decrease of numbers of species is due to the results of revisions and monographs.

In Colombia we know at present a little less than 1000 species. We can estimate that a similar number of mosses as in Colombia or Peru (900-1000) is present in Venezuela.

For comparison, we have 965 species of mosses in Canada, that means approximately the same

number as in the Andine countries over a much larger area, and there are 1248 species in the whole North America north of Mexico.

Compared with a number of 45-55.000 species of flowering plants in Colombia, bryophytes count only for about 4% of the species number of flowering plants, which makes them more easily usable.

The basis for any diversity studies are checklists! It is also the basis for any bryological studies in the tropics to know what is known from a region or country. Therefore checklists are not only useful but essential. A list of checklists from tropical countries is given in the appendix. Because checklists are lacking for many countries (at least actual ones), instructions how to compile a checklist are also given in the appendix.

The oldest bryogeography textbook was written by Herzog (1924). It included chapters on the autecology (still valid), types of ranges and descriptions of floristic realms, which are outdated in many respects. This is result of the increased knowledge of tropical bryophytes. Example: Herzog knew only about disjunctions between South America and Africa on the genus level; this is a result of old taxonomist (e.g. Carl Müller), who described (for religious reasons) the same species from different parts of the tropics under different names or bryologists having relatively uncritically described bryophytes from all over the world (Brotherus, Dixon, Thériot,

Cardot etc.). Worldwide (!) revisions in the past decades revealed, however, an increasing number of species identical in the Neotropics and Africa (and other parts of the world). Furthermore, Herzog did not consider (as all contemporary colleagues) aspects of the plate tectonics, although Wegener's continental drift theory was published already 10 years earlier but was not accepted at that time.

A modern, long but also lengthy and eloquent overlook of the phytogeography of bryophytes is found in Schuster (1983). It has, however, kept in mind that phytogeographical „explanations“ based on the shape of ranges are always hypothetical. Only recently proofs of these hypotheses are possible by molecular studies, e.g. by determination of genetic distances between disjunct populations.

Herzog, Th. 1924. *Geographie der Moose*. Fischer, Jena 439 pp.

Schuster, R.M. 1983. Phytogeography of the bryophyta. Pp. 463-626 in R.M. Schuster (ed.) *New Manual of Bryology*, Nichinan.

8.1. General tropical bryogeography (with contributions by T. Pócs)

8.1.1 Endemism

The rate of endemism is much higher in the tropics than in the extratropics but always much lower than endemism of vascular plants:

	Vasc.	Bryoph.
Galapagos Islands	50%	10%
Cuba	50%	12%
Kilimanjaro		6%
Usambara Mtns.		3%
Réunion		9%
Mauritius		6%

The rate of endemism varies in different taxonomic groups, e.g. in Western Melanesia (Piippo 1994):

Lepidoziaceae	27%
---------------	-----

Jungermanniaceae	25%
Plagiochilaceae	55%
Schistochilaceae	74%
Frullaniaceae	61%
Metzgeriaceae	28%
Herbertaceae	0%
Cephaloziaceae	0%
Pallaviciniaceae	0%
Marchantiaceae	0%

In total, 168 out of 440 species of hepatics are endemic in Western Melanesia (38.2%) - more than 50% occur in the montane forest belt.

Piippo, S. 1994. Phytogeography and habitat ecology of Western Melanesian endemic Hepaticae. *J. Hattori Bot. Lab.* 75: 275-293.

Piippo, S., T. Koppen, and D. H. Norris. 1987. Endemism of the bryophyte flora in New Guinea. *Symposia Biologica Hungarica* 35:361-372.

8.1.2 Relics

Relics are called species with former continuous range, which survived in isolated situations. Reasons for the isolation are usually climate changes. As compared with flowering plants, there are relatively many examples of relics because of the fact that bryophytes are able to survive in small ecological niches, e.g. rock fissures.

There are several cases of relics:

1. Species with tropical affinities in the temperate zones.

Examples are *Leptoscyphus cuneifolius*, *Adelanthus decipiens*, *A. lindenbergianus*, *Teleranea nematodes*, *Lepidozia cupressina*, species which are found in the Neotropics, in the African mountains as well as in the highly oceanic parts of Europe. Some species are found in the neotropics, on the Makaronesian Islands as well as in western Europe such as *Marchesinia mackaii*, *Harpalejeunea mollerii*, *Drepanoclejeunea hamatifolia*, *Colura calyptrifolia*, *Jubula hutchinsiae*, *Plagiochila bifaria* amongst the hepatics (mainly Lejeuneaceae) and *Campylopus shawii*,

Leptodontium flexifolium and others amongst the mosses. Some tropical montane species are confined to the hyperoceanic parts of Europe (e.g. the Lejeuneaceae), others occur also in suboceanic regions (*Campylopus fragilis*, *C. flexuosus*), others also in dry regions (*Campylopus pilifer*). Some species with main occurrence in the tropics are found in the southern Alps (e.g. *Braunia alopecura*), others (*Calymperes erosum*, *Trematodon longicollis*) around fumaroles in Italy.

It is argued that these species had a wider range in Tertiary, including Europe, and survived in Europe the glaciations of the Quaternary along the coast of the Atlantic Ocean. (Since the sea level was 170 m lower at that time, presumably in regions which are now inundated.) In situ survival in the southern Alps is unlikely because the habitats of these species were glaciated, if it is not assumed that they are „migration relics“ and survived there in other places.

2. Temperate, boreal and arctic species in the tropical mountains.

This concerns especially the New World, where a continuous mountain range from Alaska to Tierra del Fuego allows migration of species in different altitudes from North to South and vice versa. See also Gradstein & Vana (1987, 1994). In Africa, some temperate and mediterranean species are found on mountains, usually above 3000 m. An explanation could be that these species have moved south during Quaternary, when Europe was glaciated and all vegetation belts were shifted southwards. During interglacial times and after the last glaciation, these species stayed in the tropical mountains where they found appropriate ecological conditions in the according elevations. The mean annual temperatures of the localities of these species in the tropics resemble those in Europe (Frahm 1994).

3. Austral and subantarctic species in the tropics

By the same way (migration through mountain chain in South America, mountain hopping in Africa, island hopping in SE-Asia), subantarctic species were able to invade the tropical mountains. This is especially the fact for South America with its ideal conditions. In some cases,

the species as in Patagonia are found through the Andes (*Lepyrodon tomentosus*), in other cases this accompanied by speciation into new varieties, subspecies (*Monoclea gottschei* ssp. *gottschei* and ssp. *elongata*) or even species (e.g. *Chorisodontium*). The speciation of complexes of tropical species within some genera can be explained from subantarctic ancestors.

8.1.3 Disjunctions

Disjunct ranges can include (parts of) continents, islands or mountains. Reasons for disjunct occurrences include continental drift, formation of mountains by uplifting or volcanism, formation of islands by plate tectonics and volcanism. Disjunct ranges can be old (plate tectonics) or young (colonization of neovolcanic islands e.g. Galapagos islands) by long distance dispersal. It is difficult to decide whether a disjunct range is a result of long distance dispersal or a relictic occurrence. Long distance dispersal is only possible in air streams at high altitude. Spores must therefore be resistant to frost and UV-radiation. It is the merit of van Zanten (1976, 1978) (see also van Zanten & Gradstein 1987, 1988, van Zanten & Pócs 1981) having tested the ability of spores of species for long distance transport in the lab and in vivo (by carrying spores attached to a plane). Long distance dispersal can be assumed for weedy species (e.g. along roadside banks) and for alpine or subalpine species, who can easily be dispersed around the world, especially in the innertropics with the innertropical convergence (ITC, jetstream). Note: the ITC goes from East to West. A spore released in the Andes cannot be transported across the Atlantic Ocean but across the Pacific Ocean. Transport is only possible from Africa to South America.

Types of disjunctions are

A. in the tropics:

- pantropical disjunctions
- Neotropics - tropical Africa (see 7.1.3.1)
- tropical Africa - tropical SE-Asia (see 7.1.3.2)
- tropical Asia - Oceania - South America

B. in the extratropics

- amphipacific
- amphiatlantic
- gondwanalandic

bipolar disjunctions

Beside there are some worldwide scattered disjunctions, which are hard to explain. Examples: *Scopelophila cataractae* with occurrence in Japan, Java, Bolivia, Mexico, scattered localities in N-America. *Brothera leana* occurs in disjunct in North America and east Asia but was found in Malawi (Pócs 1993). Fragmented ranges can be either relics of formerly continuous ranges and local extinction or occasional long distance dispersal. An important and often not considered factor in phytogeography is chance. Chance can play a rôle in all irregularities.

- Frahm, J.-P. 1994.** Scientific Results of the BRYOTROP Expedition to Zaire and Rwanda 1. The ecology of epiphytic bryophytes on Mt. Kahuzi (Zaire). *Tropical Bryology* 9: 137-152.
- Gradstein, S. Rob & Vana, Jiri, 1987.** On the occurrence of Laurasian liverworts in the Tropics, *Memoirs of the New York Botanical Garden* 45: 388-425
- Gradstein, S. R. & J. Vana, 1994.** A boreal bryophyte community in a tropical montane forest of Mexico. *Tropical Bryology* 9: 31-34.
- Pócs, T. 1982.** Examples of the significance of historical factors in the composition of bryofloras. *Beih. Nova Hedwigia* 71:305-311
- Pócs, T. 1993.** *Brothera leana* (Sull.) C. Muell., a Laurasian species in tropical Africa. *Bull. Jard. Bot. Belg.* 62: 221-224.
- Schofield, W.B., Crum, H.A., 1972.** Disjunctions in Bryophytes, *Ann. Missouri Botanical Garden* 59:174-202
- Schofield, W.B., 1974.** Bipolar disjunctive mosses in the southern hemisphere, with particular reference to New Zealand, *Journal of the Hattori Botanical Laboratory* 38:13-32
- Schuster, R.M., 1969.** Problems of antipodal distribution in lower land plants, *Taxon* 18:46-90
- Sharp, A. J. 1938.** Tropical bryophytes in the southern Appalachians. *Ann. Bryol.* 11: 141-144
- Tixier, P., 1994,** Contribution à la biogéographie

dans l'hémisphère austral distribution de quelques hépatiques tropicales. *Mémoires de la Société de Biogéographie sér. 3, 4:* 95-110.

- Van Zanten, B.O. 1976.** Preliminary report on the germination experiments designed to estimate the survival chances of moss spores during aerial transoceanic long-range dispersal in the Southern Hemisphere, with particular reference to New Zealand, *Journal of the Hattori Botanical Laboratory* 44:455-482
- Van Zanten, B. O. 1978.** Experimental studies on trans-oceanic long-range dispersal of moss spores in the Southern hemisphere. *Journal of the Hattori. Botanical Laboratory* 44:455-482.
- Van Zanten, B. O., and S. R. Gradstein. 1987.** Feasibility and long-distance transport in Colombian hepatics, preliminary report. *Symposia Biologica Hungarica* 35: 315-322.
- Van Zanten, B.O. van & Gradstein, S.R., 1988.** Experimental dispersal geography of neotropical liverworts. *Beih. Nova Hedwigia* 90: 41-94
- Van Zanten, B. O., and T. Pócs. 1981.** Distribution and dispersal of bryophytes. *Advances in Bryology* 45: 479-562.

8.1.3.1 Disjunctions Neotropics - tropical Africa.

At present, 4103 species of mosses are known from the neotropics (Delgadillo et al. 1995) and 2939 species of mosses from tropical Africa (O'Shea 1995). That means we have about 25 % more species in the neotropics.

At present, 334 species of mosses are known to occur in the neotropics and tropical Africa. This is 8% of the neotropical mossflora (Delgadillo 1993). The number will certainly increase in the future with a better exploration of the tropics and a better knowledge. For instance, during the 4 weeks of field studies during the BRYOTROP project in Zaire and Rwanda, many species were even found new to Africa, most of which were

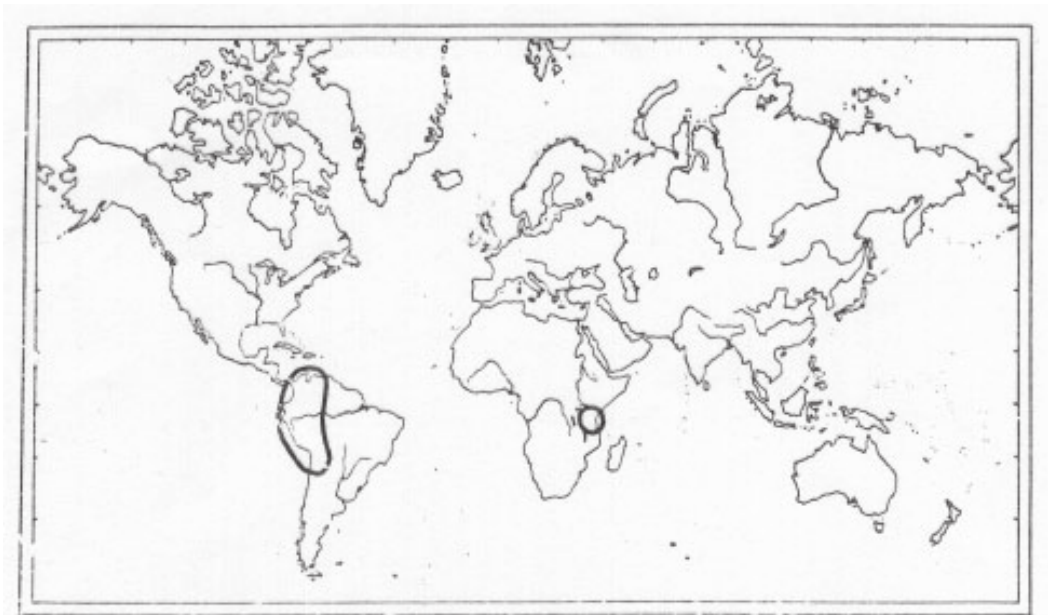


Fig. 8.1: Range of *Campylopus nivalis*, example of an African-American alpine disjunction.

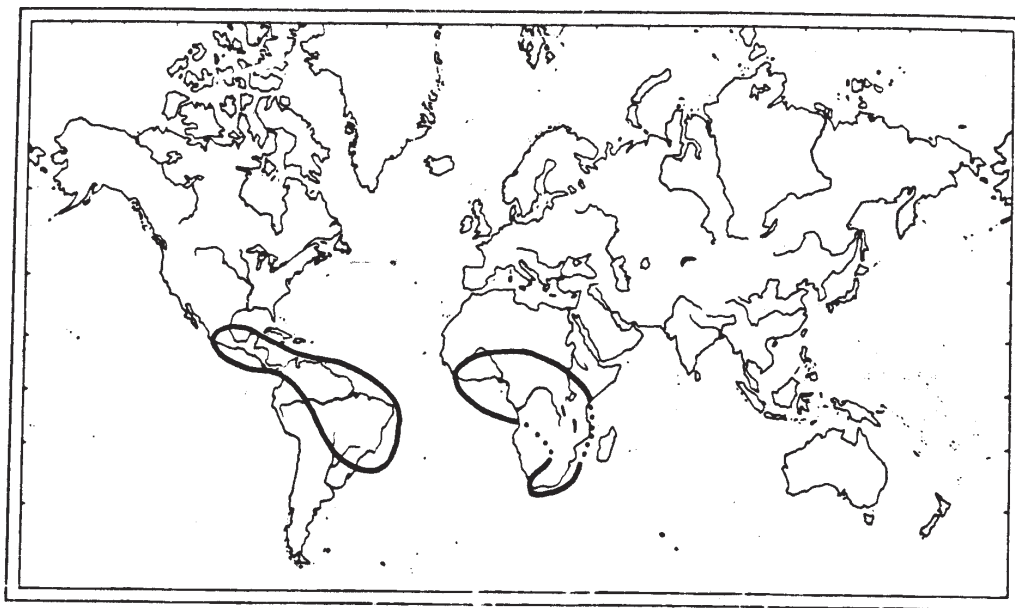


Fig. 8.2: Range of *Campylopus savannarum*, example of an African - American lowland disjunction.

known from the neotropics before.

Part of the species common in the neotropics and Africa can be dispersed by spores. This may especially count for the species in the high montane and alpine belt (fig. 8.1). However, since the main wind currents go from E to W in the tropics, it must be assumed that the species from tropical Africa reached the Andes, which is most unlikely, since the Andes can be regarded as centers for evolution of tropical montane and tropical alpine species. In this case, a spore dispersal from the Andes westwards („around the world“) to Africa must be assumed.

Another part of the species identical in tropical Africa and the neotropics is probably a remnant of the time (in Jurassic) when the continents were connected (fig. 8.2). This means they are at least 135 mio years old.

This concerns species:

- with a disjunction between Brazil and E-Africa
- species of tropical lowlands, since tier spores cannot easily get into higher air currents, and especially
- species which are sterile or produce spores not capable of long distance dispersal. Examples are: *Archidium*, e.g. the almost pantropical *A. ohioense* with a spore diameter of 250 µm; *Campylopus carolinae*, occurring in the Cerrado regions and Brazil, two localities in Rwanda and recently found in S Africa, which has lived almost buried in sand and has capsules hidden in the perichaetial leaves.

There are also vicariant taxa or subspecies in both continents showing that the mossflora of tropical Africa and the neotropics had a common origin and separate evolution took place in each continent.

Delgadillo, C.M. 1993. The Neotropical - African disjunction. *The Bryologist* 96:604-615.

Delgadillo, C., Bello, B. & Cárdenas, A. 1995. LATMOSS. A catalogue of neotropical mosses. 191 pp. Missouri Bot. Garden.

Frahm, J.-P. 1982. Grossdisjunktionen von Arealen südamerikanischer *Campylopus*-Arten. *Lindbergia* 8:36-45.

Grolle, R., 1969. Grossdisjunktionen in Artenarealen Lateinamerikanischer Leber-

moose. In: Fittkau et al. (eds.), *Biogeography and Ecology in South America* pp. 562-582. W.Junk, The Hague

Ochyra, R., Kempa, R., Buck, W.R. 2000.

Plagiothecium lucidum (Hook. f. & Wils.) Paris in tropical Africa. *Tropical Bryology* 18: 147-152.

O' Shea, 1995. Checklist of the mosses of sub-saharan Africa. *Trop. Bryol.* 10: 91-198.

Reese, W. D. , 1985 , Tropical lowland mosses disjunct between Africa and the Americas, including *Calyptothecium planifrons* (Ren. & Par.) Argent, new to the Western Hemisphere. *Acta Amazonica*, Suppl. 15(1-2): 115-121.

8.1.3.2 Disjunctions tropical Africa - tropical SE-Asia

The relations between the tropical African and SE-Asian bryofloras have been calculated by Pócs (1976, 1992). It shows that such calculations depend on the intensity of fieldwork and taxonomic studies. The first account (Pócs 1976) reported 35 species of liverworts and 73 species of mosses with this type of disjunction. The new investigation (Pócs 1992) raised the number to 70 viz. 108. Beside, there are also vicariant taxa (genera and species) in both parts. Interestingly, the affinity of the bryoflora of the neotropics and tropical Africa is less close than between tropical Africa and SE-Asia. There are 70 species of hepatics in common between tropical Africa and SE-Asia but only 52 between tropical Africa and tropical America. This result seems to support the concept of the Palaeotropics also in bryophytes. It has be kept in mind, however, that all such calculations are preliminary due to the insufficient exploration of the tropics (and thus a good motivation for such studies). The reasons for this type of disjunction has not been studied yet. Whereas South America and Africa share a common geological history, the situation in SE-Asia, which is split into many islands, is more complicated. Tropical wind systems can disperse bryophytes only from SE-Asia to Africa and not vice versa.

- Pócs, T. 1976.** Correlations between the tropical African and Asian bryofloras, I. Journal of the Hattori Botanical Laboratory 41:95-106.
- Pócs, T. , 1990.** Correlation between tropical African and Asian bryofloras. II , p 8 in: T. Koponen & J. Mänttari (eds), Congress of East Asiatic Bryology, Programme and Abstracts, University of Helsinki, Helsinki.
- Pócs, T. 1992.** Correlation between the tropical African and Asian bryofloras. II. Bryobrothera 1:35-47.

- Tan, B.C. 2002.** The affinity of Moss Floras of Japan, Taiwan and the Philippines revisited: Old problems, new insight and more questions. Acta Phytotax. Geobot. 53: 77-84.

8.1.3.3 Disjunctions Tropics - Extratropics

The floristic contrast between the tropics and the extratropics countries is much higher as between tropical regions, but much less as in phanerogams. For instance, 142 species of mosses are in common between Europe and tropical Africa and 146 species are in common between Europe and tropical America (Frahm 1995). Except for 10% cosmopolitan species, the species common in Europe and the tropics are found in the tropics in (upper) montane regions, where they have the same growth conditions as in Europe (e.g. the same mean annual temperature).

There are also few examples of tropical species in temperate regions, for example *Heterophyllum* affine from northern South and Central America, which was found several times between 1820 and 1860 in Central Europe (caused by spore dispersal by an volcanic eruption?). *Hyophila involuta*, a pantropical species from wet limestone, occurs in central Europe along the shores of some lakes (which were, however, glaciated until 13.000 years ago). The affinities between the bryophyte flora of the austral regions and tropical regions have not yet been calculated, although the austral region is considered as important phylogenetic origin for the tropical bryoflora.

- Frahm, J.-P. 1995.** Correlations between the European, tropical African, and tropical American moss floras. Fragmenta Floristica et Geobotanica 40:235-250.

8.1.4 Human influence

In contrast to Europe or North America, or parts of the southern hemisphere such as New Zealand, where introductions of bryophytes are more often recognized, an introduction of species in the tropics is less often observed but probably not less frequent. For example, *Campylopodium medium*, a species widespread in E-, SE- and austral Asia has several times been found on Puerto Rico.

Beside, many distribution patterns cannot satisfactorily be explained. This concerns for example the genus *Cinclidotus*, a genus of aquatic species endemic to Europe and the Near East, of which *C. aquaticus* was undoubtedly found near Valdivia, Chile, and *C. fontinaloides* in the Central African mountains. Thus we can offer explanations for many types of distribution (of which some may be erroneous) but not for all.

8.2 Regional bryogeography

8.2.1 Central and South America

The austral element

The oldest elements in the bryoflora of South America is the austral element, which is confined to southern Chile and southern Argentina. These regions share e.g. about 200 species of mosses with the bryoflora of New Zealand (Blöcher & Frahm 2002). This austral plant realm covers southern South America, southern Africa, southern Australia, Tasmania and New Zealand. All these regions were still connected 100 mio years ago and formed the southern coast of the Gondwana continent. Important is, that - even after separation of this continent, these regions remained in perhumid climates, providing a climatic consistency and also a floristic consistency. Although many species may have

a genetic exchange by long distance dispersal through the westwind drift (roaring forties), there are species which are not enabled to long distance dispersal because of lacking tolerance against freezing or UV-radiation. These species can be interpreted as remnants of the Gondwana flora. The austral element in South America has an importance for the Andine element in the way that the austral species were able to migrate through the Andes to Central America.

The Neotropics

As shown by fossils in Dominican amber, the basic stock of bryophyte species in the neotropics has probably originated in Tertiary as a result of long lasting periods with tropical temperatures. Except for climate changes during the Pleistocene, to which the species could at least partially adapt by migrations, this climate persisted until today. Since the neotropical realm is situated in between the holarctic and the austral plant realm, it has been invaded by elements from these both realms by a floristic pathway provided by the cordillera stretching from Alaska to Tierra del Fuego. The floristic interchange in Central America has been treated by Delgadillo (1987a,b, 1988, 1992, 1995). The Laurasian element in the neotropics were treated by Gradstein & Vana (1987, 1994). There are also neotropical bryophyte species found along the Gulf coastal plain of North America and Florida (Pursell & Reese 1970) as well as in the southern Appalachians and the Ozark Mtns. in Missouri (Sharp 1984), which may be interpreted as relicts from the Tertiary, which survived there the glacial periods.

Thanks to a compilation of species of mosses and their distribution (Delgadillo 1992), their phytogeography could be evaluated. In total, there are about 4050 species of mosses in the neotropics.

North and South America share about 675 species of mosses, which is 16.7 % of the neotropical moss flora, either with a continuous range or a disjunct distribution (Delgadillo 1995). The disjunct distribution pattern of 118 species may have originated by tectonic or climatic changes or by long distance dispersal.

Within the liverworts, endemism is almost

confined to the Jungermanniales, showing that the Metzgeriales are the more ancient element. There are over 38 genera of Jungermanniales endemic in the neotropics, often highly apomorphic or reduced (even confervoid or thalloid, or neotenic). They are typically stenotypic with only 1-3 species each and are found in the upper montane zone to the páramo (Schuster 1990). These endemic genera are derived from cool-Gondwanalandic suborders. Part of the endemics are found in the Guyana shield, a very ancient and partially isolated region. Principally, the floristic elements of bryophytes are more or less the same as those of flowering plants. There are, however, differences in the way that many bryophytes are more easily distributed and that extinctions by climatic events can be balanced by subsequent dispersal. Evaluations of types of ranges have not yet been made on a broad base. Therefore ranges of species of *Campylopus* were used (fig. 8.3). This species rich genus can serve as example and case study. In general, we can distinguish between the following floristic elements:

Neotropical element

These species are widespread from Mexico to southern Brazil, including the Caribbean, part of them extending to SE-North America (Gulf coastal plain, especially Florida, southern Alabama), where they might have been introduced by hurricanes. A part of them are not found in the Amazon lowlands since they are submontane to high-montane. Species of this distribution are present in Dominican amber with an age of about 20 mio years. Others are not found in the Andes, because they are lowland species. This is the most floristic ancient element. The lowland flora is found in the Guianas and the Amazon basin. More than 80% of the hepatic and moss flora of the Guianas belongs to this element. Accordingly, the rate of endemism is with 2.5% very low (Gradstein et al. 1990). Some of the species are also found in tropical Africa and it is an open question whether they are relicts of a former closed range (and in this case of Mesozoic origin) or distributed by long distance dispersal. A Mesozoic origin is supported by the fact that these are often species from dry habitats (savannahs, cerrados).

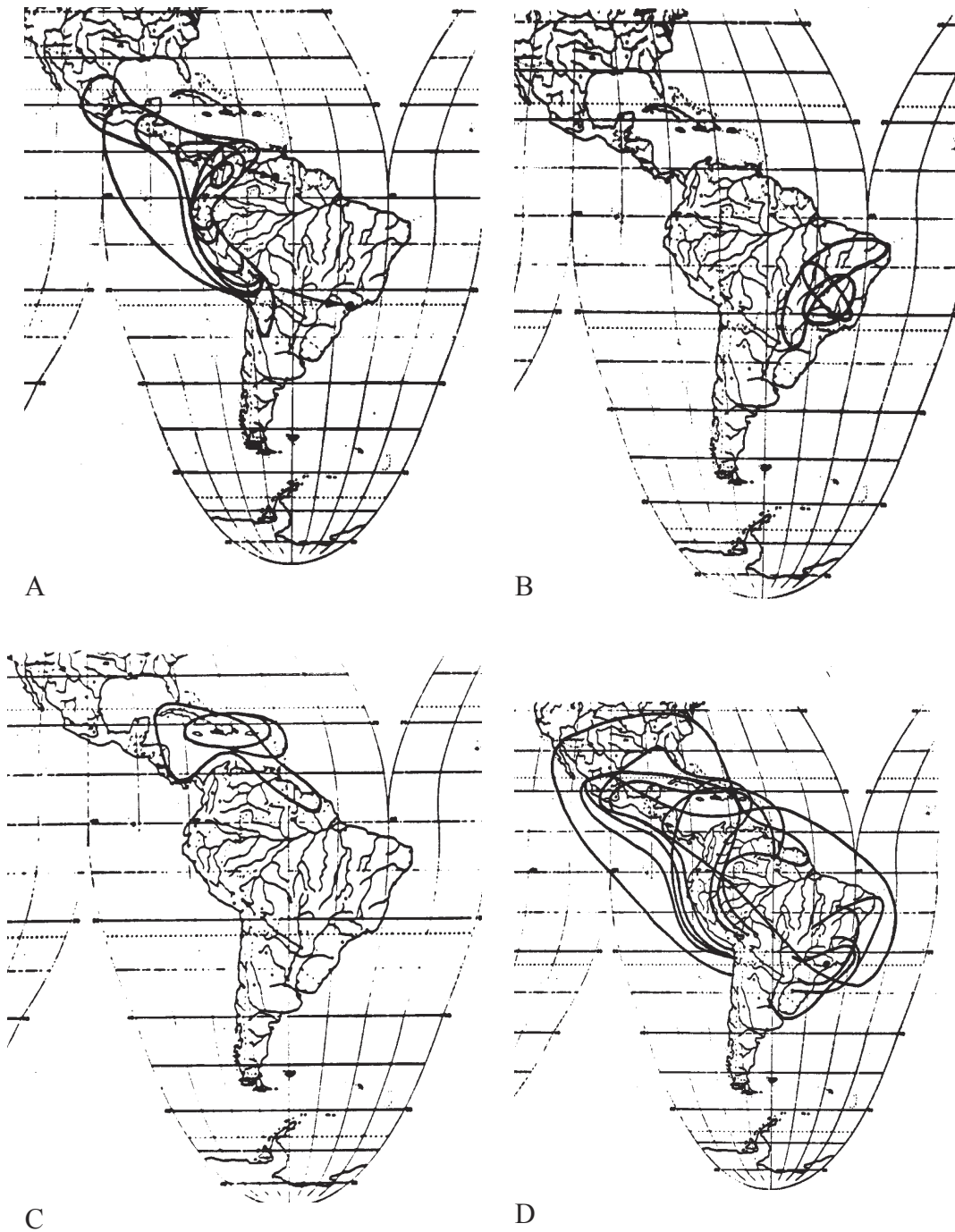


Fig. 8.3.: Distribution patterns in the Neotropics based on species ranges of the genus *Campylopus*. A. andine, B. SE-Brazilian, C. caribbean, D. neotropic.

An important impact on the present distribution may have had the climatic fluctuations during the Quaternary. During the cold periods, the savannahs expanded and the rain forests areas were retreated to small isolated parts, in which the rain forest flora and fauna survived. This effect was postulated by the German ornithologist Haffer, who introduced the „refuge theory“ based on the distribution of endemic birds and centers of diversity of birds. It was later confirmed by palaeoclimatological data, applied by phanerogamists and even applied in tropical Africa and Australia, but not yet really used in bryogeography except an attempt made by Frahm (1990). These (about 8) refuge areas are „hot spots“ for biodiversity of other organisms, because many species were not able to expand their ranges after the cool period with the rain forest, which possibly also concerns bryophytes. One of these „hot spots“ for phanerogamists is the Chocó region at the pacific slope of the Andes of Columbia. The rain forests species shall here be trapped between the ocean and the alpine by the uplift of the Andes, causing a high rate of endemism in plants, birds and butterflies. It is also the place with the highest precipitation in the neotropics (12-15 m/yr). Only few bryophytes were known from that region (31 species in the Dept. Chocó). A analysis based on floristic studies in 10 hectar plots in various altitudes financed by the National Geographic Society revealed that 60% of the mosses are widely neotropical in distribution, 12% are pantropical to cosmopolitan, 6.6% are andine, 15% are meso-american, which come down from the coast of the Caribbean and the darien gap (Frahm 1994). Only three recently described (all epiphytic) species of mosses are endemic to that phytogeographical regions, in contrast to the high rates of endemism of flowering plants. This outlines that bryophytes are genetically more conservatice and are not evolving as fast as the flowering plants (which are almost 200 mio years younger).

Species confined to SE-Brazil

These are either dry-adapted species of the cerrado regions or species of the coastal rainforests. A remarkable disjunction is found

in *Campylopus carolinae*, which occurs also along the coastal plains of SE North America. This is remarkable insofar as there was never a landbridge between the regions. Some of the rain forest species show disjunctions with E Africa or even India (e.g. *Campylopus controversus*). They show relations to the austral flora and are remnants of a gondwana flora, when SE-Brazil was situated beside E-Africa, Madagascar and India along the south coast of the gondwana continent. There are still species which also occur in E-Africa or Madagascar (e.g. *Campylopus controversus*, even in Sri Lanka), which must already have been present when the south Atlantic had just been opened and there was a continuous shoreline from Brazil to Madagascar, about 135 mio years ago. Other species are represented with vicariant subspecies in both regions (*Campylopus trachyblepharon* with ssp. *trachyblepharon* and ssp. *comatus*, *C. julaceus* with ssp. *julaceus* and ssp. *arbogasti*, interestingly all species from costal sand habitats), showing that there was at least a small separate evolution by isolation within this long time span. There are more examples, however, the trend to recognize every taxon on a species level wipes out any chance to demonstrate the evolutionary relations by infraspecific categories. This flora persistet in humid climatic conditions since that time. It is today isolated in the north by arid cerrado regions, to the east by lowlands from the Andes and to the south by the arid steppes from Patagonia, which explains its rate of endemism (which has not yet been calculated for all bryophyte species from that region).

Caribbean element

The West Indies have strong continental affinities, Originally it was thought that the floristic affinities are strongest with central America (Crosby 1969), but a database founded analysis showed that the affinities are strongest with South America (Delgadillo 1993). Crum & Steere (1958) and Steere (1984, 1985) stated that the moss flora of the West Indies, especially of the Greater Antilles, is more closely related to that of the sandstone and granitic mountains of Venezuela, the Guianas and eastern Brazil than to the floras of more calcareous mountains and high plateaus of northern South America, Central America,

Mexico and the southern Appalachians of the United States (Delgadillo 1993).

Generally, the endemism is higher in the Greater Antilles as in the Lesser Antilles. The rate of endemism is 12.2% in Cuba (Duarte 1982), which is comparably high for bryophytes. The flora of the Greater Antillean islands (Cuba, Jamaica, Puerto Rico, Hispaniola) is mainly determined by the geological history, by climatic changes during the pleistocene, by their altitude and the distance to the mainland. As in all island phytogeography, it has to be considered that the water level of the oceans has been 100-170 m lower during the past pleistocene glaciation periods, resulting in (sometimes) landbridges or at least closer distances to the neighbouring islands and continents. A survey of the bryogeography of the Greater Antillean islands is given by Buck (1990). Low islands such as Jamaica or Puerto Rico were submerged during their geological history and therefore have no bryogeographically significant flora as well as low biodiversity. In contrast, the bryoflora of Hispaniola was not submerged and its flora could respond to climatic changes with according variation of altitudinal ranges. All islands have a stock of widespread neotropical species plus endemic caribbean elements. Some species of the latter element are also found along the coast of the Caribbean Sea („circum-Caribbean“ in Belize, Venezuela, Suriname), where they probably have secondarily dispersed. The high altitudes of Hispaniola harbor a few temperate and boreal elements (e.g. *Aulacomnium palustre*, *Calliergon trifarium*), perhaps as relicts from cooler periods in the Pleistocene, and also a considerable amount of Andean elements (e.g. *Rhizogonium lindigii*, *Racomitrium crispulum*, *Lepyrodon tomentosus*), which underlines the role of long distance dispersal. Jamaica and Cuba are composed of limestone rocks and therefore have a limited biodiversity. The Lesser Antillean Islands are of recent volcanic origin and thus colonized from their surroundings.

Andine element

About 40% of the mosses are confined to the Andes to a smaller or larger extent. Some are very widespread and reach from southern Mexico to northern Argentina, others have narrower ranges

from Costa Rica to Ecuador, others are even confined to parts of Colombia or Ecuador. The distribution of species of higher elevations is controlled by a humidity gradient, which allows páramo species to occur only from Ecuador to Costa Rica but Puna species in a range covering Peru and Bolivia.

The Andes are a relatively young mountain chain with an estimated age between 10 mio and 3 years, when the present altitude was reached. This does not mean that we have young species in the Andes which recently evolved. These mountains provided an ideal pathway for austral species, which were able to migrate northwards in elevations with appropriate temperatures. Examples are species such as *Polytrichadelphus magellanicus*, *Lepyrodon tomentosus* or *Rhizogonium novae-hollandiae*. Forest and páramo species could migrate in warmer viz. cooler periods, since the vegetation belts had different extensions in the different climatic periods of the Pleistocene. There were changes in the altitudinal forest limit between 3300-3600 m and less than 2000 m during about 20 different colder periods, when the páramos expanded and fused to larger areas.

Some of the Andean species are also found in the Serra do Itatiaia in SE-Brazil, which they reached possibly by long distance dispersal rather than migration in colder periods.

Some of the Andean alpine bryophyte species are also found in the mountains of tropical Africa, probably caused by long distance dispersal. It must, however, be kept in mind, that the wind systems in the tropics go from E to W and that these species may have originated in Africa (or came to Africa from the Andes but across the Pacific Ocean and SE-Asia).

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- species from South America are also recorded from Africa and vice versa. As for the neotropics, an analysis of distribution types has not yet made on a broad scale. Therefore the ranges of the species of *Campylopus* are again used as examples (fig. 8.4)
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8.2.2 Tropical Africa

Tropical Africa harbours at present 2788 species of mosses (O'Shea 1997, there were 2939 species indicated two years before, O'Shea 1995; as for the whole tropics, the number goes down due to taxonomic revisions). 77% of the taxa are endemic to tropical Africa. As compared with flowering plants, a percentage of 23% of species occurring also outside tropical Africa is remarkably. This percentage will increase as a result of worldwide revisions and more and more

8.2.3 Tropical Asia

Plant realms are delimited by lines of the highest floristic contrast. To determine the borders between plant realms, the changes of species and genera are calculated. This has been done for tropical Asia by Tan (2002). Tan could show that 57% of the Philippine mosses are not found in Taiwan and 64% of Taiwan mosses not in the Philippines. This strong barrier is called Merrill's Line. Within Asia, the Wallace Line is famous in zoology. It seems, however, to have not much significance for bryophytes.

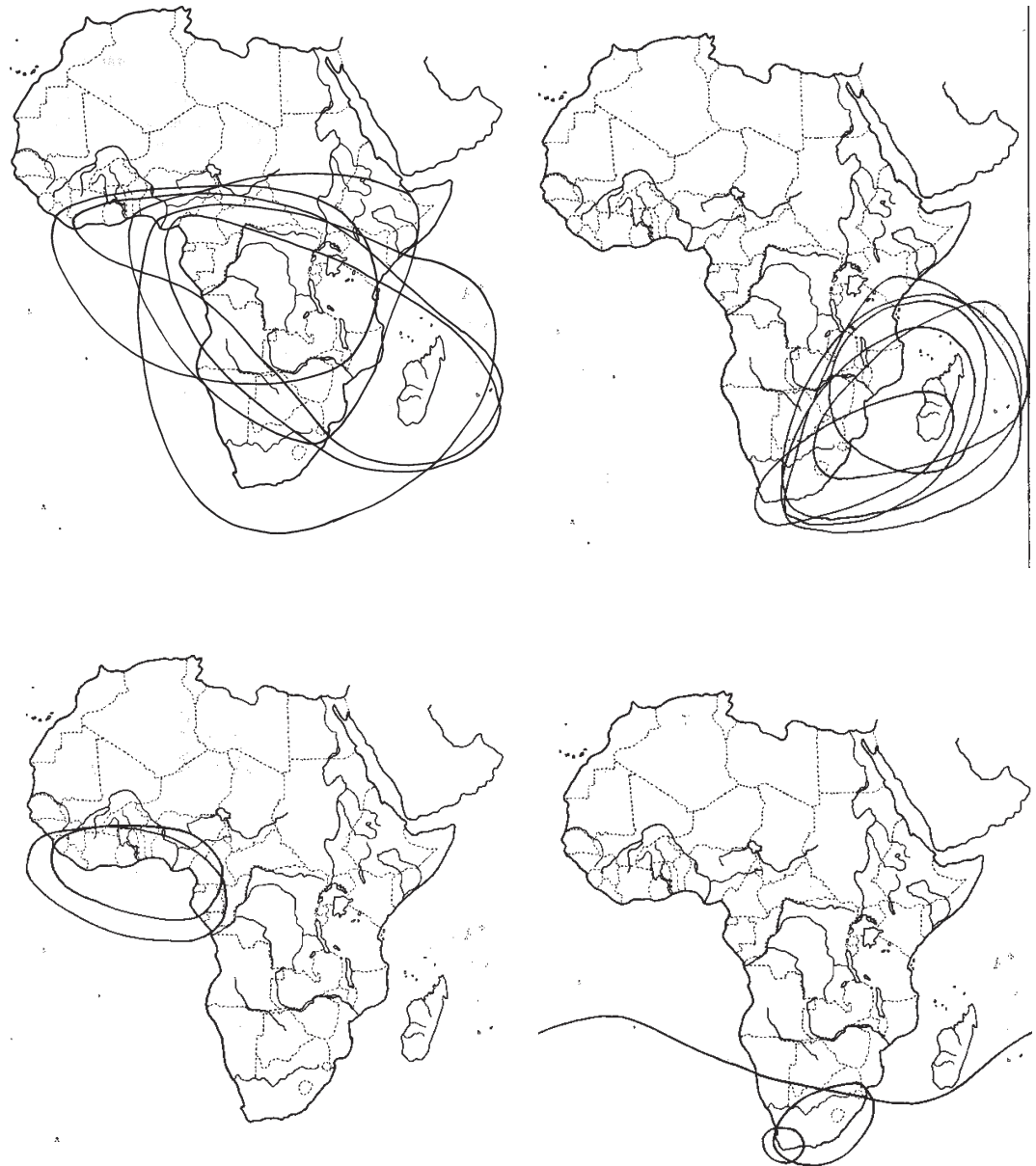


Fig. 8.4: Distribution types of African mosses exemplified by the genus *Campylopus*. A. panafrikan range, B. East African range (there are also species confined to the East African islands). C. Guinea coast range, D. subantarctic range. The afro- alpine range is not illustrated. This range includes the summits of the east African mountains as well as Mt. Kameroun.

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9. BIOINDICATION

Although bryophytes are frequently used in the northern hemisphere, especially Europe, as bioindicators for water quality, air quality, nuclear contaminations, climate change, there has been most regrettably hardly made any use of it in the tropics. Especially in the tropics, where environmental damages, air and water pollution are locally still much more relevant than in industrial countries, the use of bryophytes as bioindicators is highly recommended.

Base of this application is the fact that bryophytes as poicilohydric plants take up water and nutrients through their surface. They have no protection against toxic substances as flowering plants, which have cuticles and bark and take up water and nutrients buffered through the soil. Therefore toxic substances are automatically taken up by bryophytes, either in lakes and rivers or from the atmosphere.

The effects of air pollution on bryophytes has only be studied by Duran et al. (1992) in Mexico-City, Lisboa & Borges (1995) in Belém, Brazil, and Esciódia Ariza (1998) in Puerto Rico. Natural heavy metal accumulation has been measured by Jayasekera & Rossbach (1996). Radioactive fallout has been determined in bryophytes by Odum et al. (1970) and Steere (1970).

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Bioindication does not only concern the indication of human impact or pollution. Any bryophyte, any organism is an indicator of its habitat preferences and ranges, geographical ranges and vertical ranges. The narrower the ecological niche inhabited by a species, the better the indicator value. The indication covers parameters of soil and climate:

- nitrogen or phosphorous rich habitats indicated by *Bryum argenteum*, *Funaria calvescens* and others.
- heavy metal rich habitats indicated by species of *Mielichhoferia*, *Scopelophila*, *Merceya*.
- primary and secondary forests, disturbed and non disturbed sites (Equihua & Gradstein 1995, Hyvönen et al. 1987, Norris 1990, Romero 1999, Serrano 1996, Sillet et al. 1995).
- altitudinal belts, cloud belts (cf. chapter 6).
- phytogeographical provinces (cf. chapter 8).

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10. CONSERVATION

The sensitivity of many bryophytes to disturbance, the indication for narrow ecological niches and the rarity of many species designates bryophytes as valuable tools for nature conservation. Basis for this use is the classification into categories such as

- extinct or vanished
- endangered
- vulnerable, and
- rare, or

0 = extinct or vanished, 1 = threatened by extinction, 2 = strongly threatened, 3 = threatened, 4 = potentially threatened.

This classification requires a good knowledge of the frequency and distribution of bryophytes, which is not as good in tropical countries. However, this should not be a reason not to make use of these properties. Bryologists have to care that not only mammals, birds, orchids or bromeliads are used for nature conservation. Principally, it has to be shown to authorities that bryophytes not only exist but are valuable tools for nature conservation. So the logical consequence of a checklist, which is a necessary base, is the estimation of the frequency of species and the estimation of their threats. Even without a checklist (for a country or province), single cases of rare and endangered species can be picked up and made public to nature conservation authorities.

Such lists of threatened bryophytes, so called „red lists“, were first elaborated in Europe. The first red list was compiled for the state of Schleswig-

Holstein in Germany by Eigner & Frahm in 1974. Meanwhile almost every state in Germany as most countries of Europe have red lists. Interestingly they are not used outside Europe, although they have proved extremely useful. In Europe, the value of a region or habitat is measured by the number of endangered species occurring in this area. Therefore the presence of rare bryophytes can be used as argument for protecting areas or for the value of protected areas.

To my knowledge, there exists not yet a red list for a tropical country, which should be a stimulation to set up such lists. The purpose of Red Lists is, that not only the endangered species shall be protected but its habitat. If areas are to be considered for conservation, it is asked how many red-List-species are found in this area and by this way the value of an area is determined. The more „mossy“ a habitat is, the more urgent is it to include bryophytes in nature conservation activities. There is, however, a worldwide red list issued by the International Association of Bryologists (Tan et al. 1994), which includes 91 species. Amongst these species are mostly tropical species, which are known only from the type collection and which habitat is endangered.

In Europe, bryophyte 29 species are listed in annexe 2 of the Convention on the Conservation of European Wildlife and Natural Habitats. The European countries have lists of protected bryophyte species to a various amount, ranging

from a few endangered taxa (e.g. Sphagnum species) to all endangered red list species. Red lists can be elaborated on different geographical levels: world, continent (e.g. Europe), country and provinces. A species common in one province can be rare in another and needs protection on this regional basis. Absolute rarity exists only on a worldwide level. Therefore the most intensive efforts have to be undertaken to protect the worldwide endangered species. Thus every tropical bryologists should be orientated which species of the world red list occurs in his country, which other species are similarly endangered (this world list is surely not complete but a begin) and which efforts can be undertaken for the protection of these species. This would include not only protection of habitats („in situ“) but active steps for preservation of species, e.g. in culture („ex situ“). Similarly as endangered animals are protected in zoological gardens and rare plants in botanical gardens, it cannot be waited until certain bryophytes get extinct. Often, nature conservation has got a bureaucratic act including filling lists of endangered species, ranking the rarity and finally adding a cross mark after the species name when it has got extinct. This is administration of extinction, which should be avoided.

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Human impact and disturbance

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APPENDIX 1: COLLECTING TROPICAL BRYOPHYTES

Collecting in tropical countries officially requires usually **permits** and is usually due to severe restrictions. The conditions vary from country to country. Frahm (1996) has tried to compile the available data, which are, however, not complete and have changed in many countries since. Local botanists are not as affected as foreign botanists, for which in some cases collections are made impossible. An official argument - also used by bryologists from tropical countries - is that they are said to plunder the genetical resources of tropical countries. This is political propaganda and nonsense. Foreign botanists visiting tropical countries have, of course, to consider some points which Mori & Holm-Nilesen (1981) and Delgadillo (1987) have outlined. On the other hand it has to be kept in mind that usually and predominantly foreign botanists have done and are currently doing the botanical exploration in the tropics and most what is known about tropical bryophytes has been elaborated by foreign bryologists, else most of the tropical countries would be terra incognita.

As everywhere in the world, collecting in national parks is not allowed without permits, and permits are often only very circumstantially to apply for. Thankfully, collecting of bryophytes is much more inconspicuous as that of flowering plants (especially cacti or orchids), and there is no example known of a bryologist in tropical

countries getting problems with „inofficial“ collecting. And picking up small samples of bryophytes for identification is usually not that what even national park officials understand as plant collecting. Often bryophytes are not regarded as „real plants“

The same problems as with collecting permits concern the export of specimens, which concerns again foreign botanists and is not discussed here, because this manual is primarily addressed to tropical bryologists, which generally do not have these problems. It is important to know, that (at present) bryophytes are not on the CITES list and may be legally introduced to the homeland of the collector.

Bryophyte collecting is much easier as collecting flowering plants. Bryophytes need not to be pressed, and they need relatively little care during fieldtrips. O'Shea (1989) has written a short guide for planning collecting trips and collecting bryophytes in the tropics especially for visitors from non-tropical countries. Buck & Thiers (1996) published guidelines for collecting bryophytes in the tropics. Gradstein et al. (2001) give also instructions for that purpose. Special instructions for collecting corticolous bryophytes as well as foliicolous bryophytes and lichens are given by Gradstein et al. (1995).

There are several instructions for planning and preparing fieldtrips in tropical countries (see refs.). For visitors from non-tropical countries, there are logistic problems concerned with the style of the fieldwork such as health care, sending equipment by air cargo, car rental, staying abroad in the field, nutrition, food, which are not covered here. Another problem is the requirement of collecting permits in most countries, which have to be obtained in advance, and also eventual export permits of specimens. In this case, contact to local bryologists will be helpful. Recommendations for botanists visiting the tropics in this concern are given by Mori & Holm-Nielsen (1981) and Delgadillo (1987).

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1. Fieldstations

The easiest way to stay in the field is to use fieldstations. These fieldstations can be very differently equipped, from bamboo huts or roofs in the jungle to small labs with microscopes and dryers. The use of these stations requires, however, always official permits, which can be difficult to get. A local bryological counterpart can be very helpful in this respect, if there is somebody willing to act as such. There are often no possibilities for accommodation in the field that camping is required instead, which bears still the risk of getting robbed in parts of the tropics. Years ago, an attempt has been made to compile a list of fieldstations in the neotropics, which remained fragmentary and may be outdated today.

- Delgadillo M., C. 1989.** A Guide to fieldstations in the tropics I., Mexico. *Tropical Bryology* 1: 1-4.
- Frahm, J.-P. 1992.** A Guide to Fieldstations in the Tropics III. Colombia. *Tropical Bryology* 5: 23-26.
- Salazar Allen, N. 1989.** A Guide to fieldstations in the tropics II. Panama. *Tropical Bryology* 1: 5-8.

2. Fieldwork

Collecting bryophytes in rain forests was so far and is usually still confined to collections of trunk epiphytes below 2.5 m height or epiphylls, since there are few bryophytes on soil in rain forests. The canopy has much been neglected. By this way, only a small portion of the diversity of rain forests has been registered. This limitation has now been overcome by introducing alpine climbing techniques for canopy research (or locally by cranes, canopy walks or use of balloons). Climbing has been taught in some of our courses, but it is resigned to give instructions here, because self teaching of these climbing techniques may be too risky.

Checklist for field equipment:

Fieldbook

waterproof marker or pen with cord

altimeter and/or GPS

pocket knife with cord

paperbags

bagpack

1. Locality data. As for collecting of every biological specimen, note the locality data in a notebook with hard cover. This is done with a fine waterproof marker or a special pens („astronauts pens“, Fisher pen) with allow to write even on wet paper. Pens are easily lost in the field, so have spare pens or attach the pen to a cord and wear it around the neck or fix it at your belt. Every collecting spot gets a number. The notes include

- the locality (state, county, parish, road from... to... kilometer ..., geographical coordinates, today easily taken from a GPS). The data should allow somebody else to localize the place, e.g. a local botanist to refine a species or a monographer to map it. For the latter purpose, geographical coordinates are best, else indication of the next city found on a world atlas (e.g. 45 km NE of Bogotá). This is more valuable (for this purpose) than the indication of villages which nobody will find on a map. Military recording systems such as the UTM system not really been used by botanists, although they allow to determine every place on the world by special maps. National grid systems are useful for national grid mapping.

- the habitat.

- the elevation. Barometric altimeters can only be trusted if they are corrected every day and even during a day, the air pressure can change due to changing weather conditions that the readings are not correct. The change of one millibar airpressure results in a change of 7 m altitude reading! Today, wrist watches with built in altimeters are even cheaper than separate altimeters. Electronic altimeters are better shock-proof than mechanical altimeters (such as the famous swiss Thommen). Satallite navigators can give the altitude if 4 satellites are available; they are only as exact as 100 m (as you can see from the altitude, which goes up and down even if you stand in a place). If the place is known, the altitude is best taken from a map (if available).

- date.

2. Collecting. The bryophytes are removed from the substrate by hand or a knife. (These knives are often lost, there for use cheap ones or attach it by a chain to your belt). Very convenient is the use of scrapers, which can be bought in do-it-yourself-shops for very few money (buy half a dozen, they disappear within the time, but 50 cost as much as a swiss knife), especially to remove bryophytes from soil. For better drying, the water is removed by pressing the specimen with the hand, removing soil or litter, and flattening the specimen. Cushions are cut in slices. The specimen is put in a paper bag (small brown paper bags used in shops in the Americas, paper lunch bags elsewhere). If no bags are available, folded double (!) layers of newspaper can be used. Every specimen gets a number with a marker, usually and preferably the collectors consecutive number. There are also systems in use with a combination of the date (02041523 = 23. specimen on April 15th, 2002), country code or locality codes (e.g. CR 31/17 = 17th specimen on locality 31 during the Costa Rica trip). At least the locality number is necessary, specimen numbers can also be added later. In addition, the microhabitat has to be noted on the paper bag, for which abbreviations may be used (e.g. ct: corticolous, ru: rupestral, ep: epiphyllous, tc: terricolous).

The use of plastic collecting bags should be avoided, even for short time. The physiological problem is that wet specimen are metabolic active and start to dissimilate oif they have no light and no CO₂. This causes severe damages. Even if it is intended to cultivate the specimen later, it is recommended that they are transported dry. This concerns also transport e.g. by air mail. It is part of the bryophyte life strategy that the plants can stand dry periods in anabiosis. Ypou may start a culture easily with a dry specimen which is soaked or sprayed with water after transport.

3. Storing. During the day, the specimens are kept in a net or bagpack. If the specimens cannot be dried soon, they can be stored in nets (plastic nets) or cotton bags (flour bags, pillows, blankets), but never in plastic bags (except for protection against rainfall). Some authors have recommended to use plastic bags filled with silica gel, but the amount of water in the specimen is so much that kilograms of silica gel must be used

4. Drying. Specimens can be dried in between in the sun. Spreading the specimens on the soil makes problems during windy weather. In this case, the specimens can be hung up in their nets for drying, or can be spread in tents, if these have mosquito nets and the air can pass through the tent. If the weather does not allow or the days are used for field studies, they can be dried in the evening over kerosine or butane stoves. Croat (1979) gave instructions for a propane heater mounted on a pick-up truck. The easiest arrangement is the place a metal bar (e.g. from a plant press) over two aluminium boxes, stones, walls made from stones (like a barbecue grill), put the wet specimens on the bar and place a kerosine stove below. For this purpose, the construction of light weight aluminium frames have also be recommended (Frahm & Gradstein 1986). In the lab, similar frames can be used for drying specimens. They can be heated by electric radiators placed below or by electric bulbs mounted at the bottom of wooden boxes (bulb dryer). Greene (1986) recommended the use of silica gel for drying. In my experience, the amount of silica gel required to dry wet specimens is enormous and raises weight and storage problems. In addition, the problem raises how to get the silica dry. The use of silica gel is, however, recommended for **specimens for DNA extraction**. In general, specimens for DNA extraction need to dry up fast, that the protein chains get not broken. If the specimen is kept wet for a longer time during the trip, especially in plastic bags, it starts to mould, resulting in a degeneration of proteins. The ability of older herbarium specimens for later DNA extraction depends on the way they have been dried. Specimens which were properly dried can even be extracted after 20 years, those having not properly dried can no more be used. Therefore a quick desiccation is required. The quickest is shock drying in silica gel. For that purpose, 50 or 100 ml plastic bottles are filled 3/4 with silica gel. Next several single bryophyte plants are picked up with tweezers, put upon the silica gel and the bottle is closed. The silica gel immediately extracts all humidity from the plants, which is a guarantee for a successful extraction. If no silica gel can be used, the specimens must carefully be dried else.

If the specimens are dry, they are sealed in plastic bags. Litter bags are convenient for that purpose.

Croat, T. B. 1979. Use of a portable propane gas oven for field drying plants. *Taxon* 28:573-580.

Frahm, J.-P., and S. R. Gradstein. 1986. An apparatus for drying bryophytes in the field. *Bryological Times* 38:5.

Greene, S. W. 1986. Keeping them dry. *Bryological Times* 38:6.

Howard, R. A., Howard, E. S. 1981 Labels for wet tropical research. *Biotropica* 13: 77-78.

Special instructions for collecting epiphylls

Special instructions for collecting epiphyllous bryophytes are given by Lücking & Lücking (1996). Epiphyllous bryophytes are collected with adhaerent leaves and thus the same drying techniques as for leaves are used, at the best in small plant presses. They can be made from iron bars or wooden plates in the size of folded newspaper. Although special drying cartoon is available, newspaper can be more easily obtained and exchanged. A good trick is to insert pieces of cardboard of the same size between the newspaper sheets. by this way, the humidity soaked up from the leaves by the newspaper is soaked up the the cardboard and can evaporate through the wholes in the cardboard to both sides. If epiphylls are collected as saide collection, leaves or part of them may also be put in paper bags. From large leaves, small portions are cut. To cover the whole diversity, the collection of numerous leaves is necessary. According to R. & A. Lücking, the collection of 9 leaves in a low diversity area in Costa Rica (with a total of 48 epiphyllous species) resulted in 50% of the species, but 90% of the species were only reached by the collection of 62 leaves. In a high diversity area, 360 leaves were necessary to get 90% of the species. Epiphylls are especially found in the understory of the forests (often with a sharp upper delimitation in 1 m height) or in light gaps and along creeks. Both reflects the physiological problems of epiphylls in the tropical forest: light intensity in the understory of such forests is

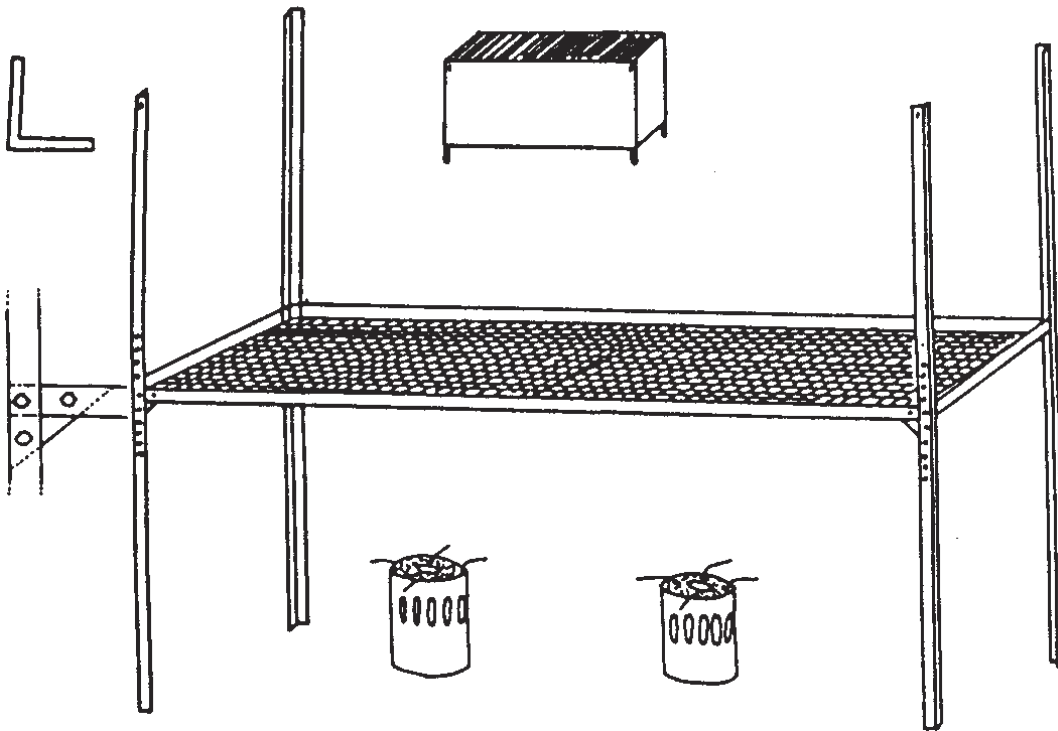


Fig. I.1: A portable drier made from an aluminium frame, heated with kerosine stoves (Frahm Frahm & Gradstein 1986).



Fig. I.2: Drying specimens in the field over a kerosine stove (BRYOTROP Peru).



Fig. I.3: Dryer from fig. I.1 in action, front removed to show the stoves (Irangi, Congo, former fieldstation of King Leopold II).

extremely low, reaching hardly the compensation point. This effect is compensated by (a) higher CO_2 (which is produced by the decomposition of litter at the forest ground, heavier as air and thus concentrated at the bottom of the forest, or (b) by higher light intensity as in light gaps.

Epiphylls are found on all kind of leaves such thick leathery leaves, leaves of palms, ferns and even filmy ferns. Only hairy leaves are not colonized. Usually, the species cannot be identified in the field nor properly distinguished. Therefore at random collections have to be made to cover most of the species. This means that collection of each 5 leaves with the highest cover of epiphylls should be taken from different phorophyte species and in different microhabitats.

The evaluation of composition, cover, abundance, frequency etc. of epiphylls on leaves is a special subject, for which special literature

(e.g. Pócs 1978, Winkler 1967) should be consulted.

Lücking, R., Lücking, A. 1996. Foliicolous bryophytes and lichens. In: Gradstein, S. R., P. Hietz, R. Lücking, A. Lücking, H. J. M. Sipman, H. F. M. Vester, J. Wolf, and E. Gardette. How to sample the epiphytic diversity of tropical rainforests. *Ecotropica* 2:59-72.

Pócs, T. 1978. Epiphyllous communities and their distribution in East Africa. *Bryoph. Bibl.* 13: 681-713.

Winkler, S. 1967. Die epiphyllen Moose der Nebelwälder von El Salvador, C.A. *Rev. Bryol. Lichénol.* 35: 303-369.

3. Fieldwork

Hectareplot studies

Collecting should preferably not be at random. In the past, collecting in the tropics was usually done by travelling around, collecting here along a roadside and there beside a waterfall. Collecting was done mostly for taxonomic purposes and main purpose was to detect new species. Usually nice sites were selected, ignoring a large deal of other, less attractive habitats. By this way, only a part of the bryoflora was registered. To cover all habitats in an area, the collections must be done systematically, including plantations, secondary forests, river banks etc. Today, the purpose of collecting is not only taxonomy but also diversity studies to get an impression of the richness of different habitats and thus of the value of these habitats (e.g. with concern to nature conservation). Therefore it should be intended to get complete inventories of study areas. Instead of collecting here and there in a large area, collecting everything in a small site is recommended.

An impression of the alpha-diversity of forest types or forests at different elevations can be obtained by collecting bryophytes on all available substrates (soil, trunks, lianas, shrubs) in a sample plot. The sample plot should be homogenous (avoiding disturbed areas such as roadside vegetation, mixtures of open and shaded sites)

to allow comparison. It is often recommended to test the size of the plots with a minimum species area curve. This is, however, only possible for very experienced collectors who can differentiate all species. Based on previous studies, the average size of the plots is generally at least 25 x 25 m and maximally 100 x 100 m. The plots need not to be quadrate but can be rectangular (e.g. 10 x 100 m), depending on the topography. It must be homogenous. In practice, the size of one hectare has revealed as appropriate. Since many studies are made on a hectare basis, the results can also be easily compared.

Transect studies

Collecting is preferably done along an ecological gradient along a transect. Such transects can lead from a ridge to the bottom of a valley (dry - moist), or go along a mountain slope (warm - cool). In this case, the floristic results can be compared with of measurements of ecological parameter und used for correlation analysis to see which factors are important for the composition of bryophytes. Recent studies preferred altitudinal gradients (e.g. the BRYOTROP project) in intervals of 200 m from the lowland to the forest line.

It is very important for all evaluations that the study areas are comparable (not only in size but also in structure) that not „apples are compared with pears“.

Epiphyte and Canopy studies

Special instructions for collecting epiphytic bryophytes are given by Gradstein (1996). A large part of the diversity of rain forests is harboured in the crowns of trees. This does also concern bryophytes, to a smaller content in the lowland forests but increasingly in montane forests. Part of the species is even restricted to the crown. Trees are usually climbed using the rope technique or (if possible) the canopy is accessed by a crane, canopy walk, or balloon. Rope technique is described by e.g. ter Steege & Cornelissen (1988). Exceptionally, „destructive collecting technique“ can be used by cutting a tree. Also fallen trees should be studied, which have come down not too long time ago. Within the tree, inventories are made of 20 cm² plots within the 5-6 tree zones (Johannson 1974) in a

sufficient number so that a statistical evaluation will be possible. The outer canopy branches have to be sawed off and lowered to the ground by ropes for study. If possible and allowed, also large branches can be sawed off and studied more comfortably on the ground. The inventory is made based on the Johannson-zones (Johannson 1974). It is often recommended to study a number of plots of 20 x 20 cm within every Johannson zone. This is essential for all further statistics, since the calculations must be based on a same area. To cover all species, the number of plots must be quite high. If no statistics are intended, collecting larger parts of trunks and branches is recommended, because some species may just occur outside the sample plots.

Another method is, to take all bryophytes from a sample plot of 20 x 20 cm in the lab. This is sometimes required, if the wheather or attacks from leeches, ants or mosquitos do not allow to perform longer studies in the field. The removed cover can be transported in pizza boxes. In the lab, the samples can be studied under the binocular. This method can be performed only if the epiphyte cover has a certain thickness and not for crust epiphytes, but is recommended for phytoisocological studies.

Depending on the purpose of the study, the species are registered as presence/absence (for diversity studies) or their cover is estimated (for phytosociological studies), either by percentage or by Braun-Blanquet indices. Presence/absence does nothing say about the different abundance of species and gives no idea of the composition. A present species can be a tiny liverwort interwoven in a moss or a moss covering most of the branch or trunk.

For trunk epiphytes, trees with different bark structure should be studied. In opposite to trees in temperate regions, the pH of the bark varies not much and is always low (between 4 and 6). Species composition is influenced by the structure of the bark (smooth, flacy, stripping off) and thre water stroing capacity of the bark. The higher the precipitation of an region, the lower is the influence of bark factors.

Cornelissen, J.H.C. & ter Steege, H. 1989. Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen

forest of Guyana. *J. Trop. Ecol.* 5: 131-150.

- Gradstein, S.R. 1996.** Corticolous bryophytes. In: Gradstein, S. R., P. Hietz, R. Lücking, A. Lücking, H. J. M. Sipman, H. F. M. Vester, J. Wolf, and E. Gardette. How to sample the epiphytic diversity of tropical rainforests. *Ecotropica* 2:59-72.
- Johannson, D. 1974.** Ecology of vascular epiphytes in West African rain forest. *Acta Phytogeogr. Suecica* 59: 1-136.
- Ter Steege, H., Cornelissen, J.H. 1988.** Collecting and studying bryophytes in the canopy of standing rain forest trees. Pp. 285-290 in: J.M. Glime (ed.) *Methods in Bryology*. Nichinan.

APPENDIX II: HERBARIUM MANAGERMENTS

1. Drying

If the collections arrive in the herbarium in wet state, they need to be dried up immediately. Some herbaria have special dryer of various modes. Some consist of boxes, open above, in which the plant presses are upright packed. Heat is generated by light bulbs below. The warm air rises through the cardboard between the specimens. A similar construction as the field drier or the field drier itself as described in Appendix I (4) can also be used in the lab and an electric heater can be used instead of the kerosine stove. Other drier consists of a cupboard with shelves made from wire and integrated heater, through which hot air is blown. However, bryophytes do not need so much care. The simplest and easiest way is to spread the specimens in a room in one layer and wait until they are dried.

Bryophytes are rarely attacked by pests. Reason is that they contain antifeeding agents, with which they protect themselves against being eaten up by beetles and snails. Therefore the chance being attacked by e.g. museum beetles is low, even in the tropics. But every rule is without exception. There are, nevertheless, specialists among beetles which can eat bryophytes. I have seen in my life only one case (in a private herbarium in Germany!). Therefore protective treatments can be performed. The classic method is chemical poisoning of the specimens., which is

problematical, since chemicals which poison beetles are also harmful for men. Some herbaria still poison with naphthalene, which causes an uncomfortable odor. The easiest way is to cool-freeze the specimens. Requirement is that the specimens are absolutely dry. Then they will be sealed in plastic bags and stored in a deep freezer at -20°C for 24 hours. Larger bags also longer. By that way, all beetles and larvae, especially tropical ones, are killed. After the freezing, they are kept in the plastic bags to warm up for again 24 hrs.

2. Labelling

Today, labelling is completely done by computers. Since the beginning of the computer era in the seventies of the last century, biologists have tried to make use of computers. At first, punch cards were used to store the collecting information. For the first PCs, special labelling software was designed, and there were numerous different programs with various advantages but also disadvantages.

Today there exist principally two ways to label specimens, (a) by using a label program, (b) to use a database program. Alternative a is not recommended, since it only allows to print labels from different localities, which is nothing better

than copying labels on a xerox machine. The advantage of database programs is that all label information is stored in the computer and can be searched for. By that way, also evaluations can be performed such as: which species were found in the same relevée?, which species were found between 6- and 800 m? which species were found on a special host tree?, in the department XY or around the village of YZ? And so on.

Any database program can be used for that purpose (e.g. MS Access, Filemaker) by generating fields for

- species
- country
- state/department
- county
- locality
- habitat
- date
- collector
- collection number
- altitude
- latitude/longitude

If a mask is generated for the outprint, the label can directly be printed to the paper sheet from which the convolute is folded. This avoids to cut and glue the labels.

Attention has also be paid to the use of paper, glue, pens and printers. Formerly, the **paper** (used for herbarium sheets, envelopes or convolutes) contained acids which caused that the paper was easily broken after hundred years or more. This required extensive procedures (re-packing) of specimens in older herbaria. Today, even xerox paper is acid free that any paper can be used for herbarium puposes and no special paper is required.

If labels are used and glued on the specimens, attention has to be paid to the kind of **glue**. Self-adhesive labels, although they seem practically, should be avoided since the glue lasts no more than 10-20 years. It is absorbed and degenerated by the paper with the result that the labels will fall off. (Sad own experience).

Problems can also arise by the use of **pens** to mark specimens with collection numbers. The ink of many ink pens is bleaching under sun light and disappearing, causing heavy problems with the identification of specimens. Ink pens should therefore not only waterproof but also permanent.

A test can clarify this: a paper sheet with some notes made by different junk pens is exposed to the sun (at the window) and the notes of non-permanent pens will dissappear soon.

Also labels must be as waterproof as the ink pens and therefore the choice of **printers** is important. Ink printer prints are not waterproof and should be avoided. In contrast, laser printer outprints will not make any problems.

Beispiele von Labels, Auswertungen

3. Storing

Traditionally, bryophyte specimens were kept in the same way as flowering plants: the convolutes were glued upon herbarium sheets, these sheets wrapped with an envelope, and the sheets bound to faszicles. This may have made sense in large herbaria, where the cabinets had the size for herbarium sheets. However, herbarium sheets with several specimens glued upon one sheet are circumstantial to handle. If the convolutes are glued upon the sheets, they can hardly be removed (e.g. after a misidentification) without damaging the specimen (this is the reason that some herbaria used needles to fix the specimens, other did not glue the specimens but laid them loosely between sheets with the consequence that specimen could easily fall out).

The proper method is today to store the specimens like filecards in cardboard boxes. Then they can easily be sorted. The only (small) disadvantage is the upright position of the specimens. The boxes are placed in metal cabinets. Fumigating is usually not necessary.

Bello y Bello, B. 1992. La colección briológica del Herbario Nacional de México (MEXU). *Tropical Bryology* 6: 35-38.

Fosberg, F. R., and M.-H. Sachet. 1965. Manual for tropical herbaria. International Bureau for Plant Taxonomy. Utrecht, The Netherlands.

BRYO AUSTRAL

Diversität, Anpassungs- und Lebensstrategien und Evolution der Bryoflora und -vegetation südhemisphärischer temperater Regenwälder

Eucamptodon perichaetiale

CHILE: X. Region, Parque Nacional Puyehue 50 km E Osorno, Sector Antillanca, nahe Centro de Ski,

Nothofagus pumilio -Wald (max. 15 m) 1050-1160 m
 Nothofagus pumilio-N. antarctica-Wald 1160 m-Waldgrenze (1200m)

Höhe (m): 1050-1200

leg. J.-P. Frahm 18.3.01. No. 30-3

Project of the Institute of Systematic Botany and Plant Geography, University of Berlin, and the Botanical Institute, University of Bonn, Germany, supported by the German Research Foundation



Fig. II.1: Herbarium label generated with the computer program Filemaker. All text is stored in fields and can be searched for and extracted for reports or evaluations.

Fig. II.2 (right): Modern storing herbarium specimens in cardboard boxes in a steel cabinet (Herbarium BONN).



Fig. II.3: Old style of bryophyte herbarium in fascicles designed for flowering plants (Hb. BONN).

APPENDIX III: IDENTIFICATION

The amount of available literature varies much in the different parts of the tropics. The situation is relatively the best in the neotropics as compared with Africa or tropical Asia. Recently, the British Bryological Society Tropical Bryology Group started to enhance the knowledge of the bryology of tropical Africa with different activities.

A first step is to identify families or genera. This is possible by generic bryophyte floras such as that by Gradstein et al. (2001) for the neotropics. A similar flora for tropical Africa is in preparation.

Next, the identification of species can be

(a) taxon-orientated by monographs or revisions of genera. A directory for monographs was published by Greene & Harrington (1988), which is now slightly outdated. For mosses, all relevant literature is found in the TROPICOS database at the Missouri Botanical Garden (www.mobot.org).

(b) flora-orientated. An account of the floristic literature of the world was given by Greene & Harrington (1989). The most relevant tropical floras are listed below. Also checklists may be consulted.

Greene, S.W., Harrington, A.J. 1988. The *Conspectus of Bryological Taxonomic Literature Part 1. Index to monographs and regional reviews.* Bryophytorum Bibliotheca 35.

Greene, S.W., Harrington, A.J. 1989. The *Conspectus of Bryological Taxonomic Literature Part 2. Guide to national and regional literature.* Bryophytorum Bibliotheca 37.

2.1 Neotropics

The neotropics are the bryologically best surveyed tropical area in the world, which is documented by a comparably and relatively high number of checklists or even floras. There exists even a generic flora for the whole neotropics (Gradstein et al. 2001). This book is a breakthrough for bryology in the neotropics. It covers a short introduction to the anatomy, morphology and systematics of bryophytes, a description of the bryophyte regions with relevant literature, a description of habitats with representative species and genera, a list of floras and a comprehensive bibliography and - as the mayor part - keys for and descriptions of hepatic and moss genera with illustrations of representative species. A comparable book for tropical Africa is under preparation by the Tropical Bryology Working Group of the British Bryological Society.

Allen, B. 1994. *Moss Flora of Central America Part 1. Sphagnaceae - Calymperaceae.* Missouri Bot. Garden.

- Allen, B. 2002.** Moss Flora of central America Part 2. Encalyptaceae - Orthotrichaceae. Missouri Bot. Garden.
- Bartram, E.B. 1949.** Mosses of Guatemala. Fieldiana (Botany) Chicago.
- Buck, W.R. 1998.** Pleurocarpous Mosses of the West Indies. Memoirs of the New York Botanical garden vol. 82, 400 pp.
- Churchill, S.P. 1994.** The Mosses of Amazonian Ecuador. AAU reports 35, Aarhus.
- Churchill, S.P., Linares, E.L. 1995.** Prodromus Bryologiae Novo-Granatensis. 2 vols. Bogotá.
- Crum, H.A. and Steere, W.C. (1957).** Mosses of Puerto Rico and the Virgin Islands. *N.Y. Academy of Sciences* 7(4). [Useful for the Caribbean.]
- Duarte-Bello, P. 1997.** Musgos de Cuba. Madrid. 717 pp.
- Florschütz, P.A. 1964.** Flora of Suriname, Musci, part I.
- Florschütz-de Waard, J. 1986.** Flora of Suriname, Musci, part II.
- Florschütz-de Waard, J. et al. 1996.** Flora of Suriname, Musci, part III. Royal Botanic Gardens Kew.
- Gradstein, S.R. (1989).** A key to the Hepaticae and Anthocerotae of Puerto Rico and the Virgin Islands. *The Bryologist* 92(3): 329-348. [A key emphasising vegetative characters for 237 species in 92 genera of liverworts and hornworts recorded from Puerto Rico and the Virgin Islands; also useful for other parts of tropical America.]
- Griffin, D. and Morales, M.I. (1983).** Keys to the genera of mosses from Costa Rica. *Brenesia* 21: 299-323. [Useful key to genera of Central America - over 200 genera are dealt with.]
- Sharp, A.J., Crum, H.A., Eckel, P.M. 1994.** The Moss Flora of Mexico. 2 vols. New York Bot. Garden.

2.2 Tropical Africa

Compiled by **Tamás Pócs** and **Brian O'Shea**

Various keys are found on the webpage of the British Bryological Society Tropical Bryology

Group: <http://britishbryologicalsociety.org.uk>.

Hepatics

- Key to African *Caudalejeunea* (Vanden Berghen, 1984)
- Key to tropical African *Frullania* (Vanden Berghen, 1976)
- Key to African species of *Jungermannia* (Vána, 1974-5)

Mosses

- Key to families of African pleurocarps (Petit, 1978)
- Keys to the Hookeriales of Africa (Demaret & P. de la Varde, 1951-5)
- Key to African Hypnaceae (Petit, 1978)
- Key to genera of African Leucobryaceae (Onraedt, 1976)
- Key to Regmatodontaceae of the world (Eakin, 1975)
- Key to African Rhachithecaceae (O'Shea, 1997)
- Key to Rhacocarpaceae of the world (Frahm, 1996)
- Key to African Rhizogoniaceae (O'Shea, 1997)
- Generic key to African Sematophyllaceae (O'Shea, 1999)
- Key to tropical African *Breutelia* (De Sloover, 1975)
- Key to African species of *Campylopus* (Frahm & O'Shea, 1996)
- Key to tropical African *Leptodontium* (De Sloover, 1987)
- A key to African *Leucophanes* (Onraedt, 1976)
- Key to African species of *Neckera* (De Sloover, 1977)
- Key to most African species of *Racomitrium*
- Key to tropical African *Schoenobryum* (Bizot & Pócs, 1982)

Pócs, T. & O'Shea, B.J. 1991. Quick Reference List of Basic Literature to Identify Tropical African Bryophytes. *Tropical Bryology* 4: 69-854.

HEPATICAE and ANTHOCEROTAE

Checklists or floras with keys, illustrations or descriptions.

Arnell, S. 1956. Hepaticae collected by O. Hedberg et al. on the East African Mountains. *Ark. f. Bot.* **3**:517-562.

Arnell, S. 1963. Hepaticae of South Africa. Stockholm, 411 pp.

Demaret, F. 1942. Prodrome des bryophytes du Congo belge et du Ruanda-Urundi. II.-Hepaticae. *Bull. Jard. Bot. Bruxelles* **16**:287.

Grolle, R. 1978. Die Lebermoose der Seychellen. *Wiss. Ztschr. Friedrich-Schiller- Univ. Jena, Math.-Nat. R.* **27**:7-17.

Jones, E.W. 1990. African Hepatics XL. An artificial key to the genera of African Hepatics. *J. Bryol.* **16**:9-40.

Jones, E.W. & Harrington, A.J. 1983. The hepatics of Sierra Leone and Ghana. *Bull. Brit. Mus. Nat. Hist. Botany* **11**:215-289.

Vanden Berghen, C. 1972. Hépatiques et anthocérotales. In Symoens, J.-J. (Ed.): Résultats scientifiques. Exploration hydrobiologique du bassin du Lac Bangweolo et du Luapula. Vol.8, fasc.1. Hépatiques et Anthocérotales. 202 pp.

Vanden Berghen, C. 1978. Hépatiques du Shaba. Corrections et additions. *Bull. Jard. Bot. Nat. Belg.* **48**:367-372.

Reference list according to taxa

Acanthocolea - Kruijt, R.H.C. 1988:1.

Acrolejeunea - Gradstein, S.R. 1975:1.

Adelanthus - Grolle, R. 1972:325.

Allisoniella - Vána, J. 1985:86.

Alobiellopsis - Schuster, R.M. 1969:682.

Anastrophyllum - Vána, J. 1982:72.

Andrewsianthus - Grolle, R. 1963:437; Vána, J. 1980:228.

Aneura - Meenks, J.L.D. & Pócs, T. 1985:79.

Anomalolejeunea see under Cheilolejeunea

Aphanolejeunea - Pócs, T. 1984b:239.

Arachniopsis see under LEPIDOZIACEAE/LEPIDOZIOIDEAE

Archilejeunea - Vanden Berghen, C. 1951c:112.

Bazzania - Arnell, S. 1965:66 (Madag-Masc.); Jones, E.W. 1975:299, 1980:312; Onraedt, M. 1977:139 (Madag-Masc).

Brachiolejeunea see most African species under Frullanoides, but consult **van Slageren, M. 1985.**

Bryopteris - Stotler, R.E. & Crandall-Stotler, B. 1974:1.

Calycularia - Jones, E.W. 1985b:497.

Calypogeia - Bischler, H. 1970:63, Jones, E.W. 1976b:43.

Capillolejeunea - Arnell, S. 1965:69.

Caudalejeunea - Vanden Berghen, C. 1948:764; 1972:432; 1984:99; Jones, E.W. 1953c:164.

Cephalojonesia - Grolle, R. & Vanden Berghen, C. 1970b:764; Jones, E.W. 1987:503.

Cephalozia - Vána, J. 1988:179.

Cephaloziella - Jones, E.W. 1958:430. (lowland species).

Ceratolejeunea - Vanden Berghen, C. 1951a:61; 1953:279; 1973:381.

Chaetolejeunea see under Rectolejeunea

- Chandonanthus** - Vanden Berghen, C. 1965:135.
- Cheilolejeunea** - Grolle, R. 1979:343; Jones, E.W. 1954b:380, 1973:548, 1976b:49, 1982:37.
- Cheilolejeunea/Anomalolejeunea** - Vanden Berghen, C. 1951d:364, 1953:278.
- Cheilolejeunea/Euosmolejeunea** - Jones, E.W. 1954a:375, 1973:551; Vanden Berghen, C. 1965:148.
- Cheilolejeunea/Strepsilejeunea** - Jones, E.W. 1985a:395, 1988:149; Vanden Berghen, C. 1960:133.
- Chiloscyphus** - Grolle, R. 1984:505; Jones, E.W. 1953d:172.
- Chonecolea** - Jones, E.W. 1985b:498.
- Cladolejeunea** - Zwickel, W. 1933:112.
- Clasmatocolea** - Engel, J.J. 1980:1; Grolle, R. 1960:78.; Grolle, R. & Vanden Berghen, C. 1970:385; Jones, E.W. 1987b:503.
- Cololejeunea** - Jones, E.W. 1954e:408; Pócs, T. 1975:353; 1980:305; 1985:113; Tixier, P. 1977:173 (Madagascan spp.); 1979:602.
- Cololejeunea** - species with acute leaves - Vanden Berghen, C. 1977:235.
- Cololejeunea** - species with dentate leaves - Jones, E.W. 1953b:158.
- Cololejeunea** - species with hyaline leaf margin - Jones, E.W. 1953a:144; Vanden Berghen, C. 1972:467.
- Cololejeunea** - species with papillate leaf margin - Vanden Berghen, C. 1977:232.
- Cololejeunea** - species with papillose dorsal leaf surface - Vanden Berghen, C. 1977:239.
- Cololejeunea/Lasiolejeunea** - Tixier, P. 1985:177.
- Cololejeunea/Pedinolejeunea** - Tixier, P. 1985:15.
- Cololejeunea/Taeniolejeunea** - Benedix, E.H. 1953; Jones, E.W. 1968b:569.
- Colura** - Jones, E.W. & Pócs, T. 1987:495; Jovet-Ast, S. 1953:206; 1954:1; 1956:272; 1958:19; 1976:909; 1980:277.
- Conoscyphus** - Engel, J.J. 1987:533; Piippo, S. 1985:129.
- Cyathodium** - Jones, E.W. 1952:55; Jovet-Ast, S. 1970:57.
- Cylindrocolea** - Jones, E.W. 1976b:46.
- Dicranolejeunea** - Jones, E.W. 1970a:72.
- Diplasiolejeunea** - Jones, E.W. 1973:552; Tixier, P. 1977:117; 1980:743; 1984:11; 1987:219; Vanden Berghen, C. 1960:119; 1977:216.
- Diplasiolejeunea/Pellucidae** - Jones, E.W. 1954c:393; Tixier, P. 1985:331.
- Drepanolejeunea** - Jones, E.W. 1968b:567; Vanden Berghen, C. 1961:61.
- Drepanolejeunea/Kolpolejeunea** - Grolle, R. 1976:191.
- Euosmolejeunea* see under *Cheilolejeunea*
- Evansiolejeunea** - Vanden Berghen, C. 1965:151.
- Exormotheca** - Schiffner, V. 1942:40.
- Frullania** - Vanden Berghen, C. 1976c:1; 1976b:335; 1982:207 (Madagascan species).
- Frullanoides** - van Slageren, M. 1985. (covers previous African *Brachiolejeunea*); Jones, E.W. 1968b:565; Vanden Berghen, C. 1951b:87; 1978:124.
- Gongylanthus** - Jones, E.W. 1964:649.

- Gottschea see under Schistochila
- Gottschelia** - Grolle, R. 1968:13.
- Gymnocoleopsis** - Vána, J. 1982:79.
- Gymnomitrium** or -um - Vána, J. 1985:88.
- Harpalejeunea** - Arnell, S. 1965:75.
- Hygrolejeunea see under Lejeunea
- Inflatolejeunea see under Lejeunea
- Isotachis** - Vána, J. 1982:63; Vanden Berghen, C. 1965:130.
- Iwatsukia** - Grolle, R. & Onraedt, M. 1974:232; Vána, J. 1980:233.
- Jamesoniella** - Grolle, R. 1971:1.
- Jungermannia** - Vána, J. 1974:277; 1975:357.
- Kurzia see under LEPIDOZIACEAE/LEPIDOZIOIDEAE
- Lejeunea** - Jones, E.W. 1979:389; 1984:159; 1985a:385.
- Lejeunea** - *L. eckloniana* complex - Jones, E.W. 1974b:77.
- Lejeunea** - *L. flava* complex - Jones, E.W. 1968a:548.
- Lejeunea** - *L. caespitosa* group (small, monoecious species) - Jones, E.W. 1972:36.
- Lejeunea** - (small, dioecious species) - Jones, E.W. 1972:23; 1989:665.
- Lejeunea/Chaetolejeunea see under Rectolejeunea
- Lejeunea/Cladolejeunea see under Cladolejeunea
- Lejeunea/Hygrolejeunea** - Vanden Berghen, C. 1961:65; 1972:438; 1977:202.
- Lejeunea/Inflatolejeunea** - Vanden Berghen, C. 1965:147.
- Lejeunea/Microlejeunea see under Microlejeunea
- Lejeunea/Pleurolejeunea** - Jones, E.W. 1969:787.
- Lejeunea/Umbilicatae** (species with eplicate perianth) - Jones, E.W. 1967:299.
- LEJEUNEACEAE** - Schuster, R.M. 1963. (generic key with annotations).
- LEJEUNEACEAE/PTYCHANTHOIDEAE** - Gradstein, S.R. 1985:13.
- Lepidozia see under LEPIDOZIACEAE/LEPIDOZIOIDEAE
- LEPIDOZIACEAE/LEPIDOZIOIDEAE** - Pócs, T. 1984a. (discusses nomenclature & distribution of African Arachniopsis, Kurzia, Lepidozia, Psiloclada, Sprucella and Telaranea).
- Leptocolea see Cololejeunea
- Leptolejeunea** - Vanden Berghen, C. 1961:58; 1963(1964):49; 1977:213.
- Leptoscyphus** - Grolle, R. 1962:1; Jones, E.W. 1953d:196.
- Leucolejeunea** - Jones, E.W. 1973:545.
- Lophocolea see under Chiloscaphus
- Lopholejeunea** - Vanden Berghen, C. 1978:123; 1984a:393.
- Lophozia** - Vána, J. 1982:80.
- Marchantia** - Vanden Berghen, C. 1954:37.
- MARCHANTIALES** - Vanden Berghen, C. 1965:166 (generic key).
- Marchesinia** - Jones, E.W. 1970a:78; Vanden Berghen, C. 1976a:926.

- Marsupella** - Vána, J. 1985:91.
- Mastigolejeunea** - Vanden Berghen, C. 1948a:49; 1951b:90. (sub *Brachiolejeunea nigra*).
- Mastigophora** - Vanden Berghen, C. 1973:365.
- Metzgeria** - Arnell, S. 1953:107 (S.Afr. spp.); Kuwahara, Y. 1973:566; 1986:1 (although deals with Neotropic species, many records of African taxa); Vanden Berghen, C. 1948:187; 1960:111.
- Microlejeunea** - Jones, E.W. 1969:775; 1979:394; Jovet-Ast, S. 1959:191; Vanden Berghen, C. 1965:143; 1977:204.
- Nardia** - Grolle, R. 1964:297.
- Nesolejeunea* see under *Lejeunea*
- Notothylas** - Hässel de Menendez, G. 1976:19.
- Odontolejeunea** - Vanden Berghen, C. 1963(1964):52; Teeuwer, M. 1989:1.
- Odontoschisma** - Grolle, R. 1960b:207.
- Otolejeunea** - Grolle, R. 1985:45; Tixier, P. 1980a:607.
- Oxymitra** - Garside, S. 1958:83 (all species considered).
- Pallavicinia** - Grolle, R. 1984:508; Vanden Berghen, C. 1965:164.
- Paraschistochila* see under *Schistochila*
- Plagiochasma** - Bischler, H. 1978:223.
- Plagiochila** - Jones, E.W. 1962:254; 1980:13; Vanden Berghen, C. 1981:41.
- Pleurolejeunea* see under *Lejeunea*
- Porella** - Jones, E.W. 1963:446.
- Prionolejeunea** - Vanden Berghen, C. 1952:170; 1973:383; 1977:209.
- Ptychanthus** - Vanden Berghen, C. 1951e:64.
- Ptychocoleus* see under *Schiffneriolejeunea*
- Pycnolejeunea** - Grolle, R. 1979a:179; Jones, E.W. 1979:397.
- Radula** - Jones, E.W. 1977:461; Yamada, K. 1975:115.
- Rectolejeunea** - Jones, E.W. 1974a:71.
- Rectolejeunea/Chaetolejeunea** - Jones, E.W. 1969:784.
- Riccardia** - Jones, E.W. 1956:74; Meenks, J. & Pócs, T. 1985:81.
- Riccia** - Jones, E.W. 1957b:210; Gillet, H. & Jovet-Ast, S. 1957:62; Jovet-Ast, S. 1986:287 (N-Afr).
- Ricciocarpus** - Jones, E.W. 1957b:209.
- Scapania** - Arnell, S. 1957:26.
- Schiffneriolejeunea** - Jones, E.W. 1954d:396; 1982:45; Vanden Berghen, C. 1976a:925.
- Schiffneriolejeunea/Pappeanae** - Gradstein, S.R. & Vanden Berghen, C. 1985:173.
- Schistochila** - Grolle, R. & Zijlstra, G. 1984:87; Jones, E.W. 1976a:33.
- Sprucella** - Vanden Berghen, C. 1946:91; 1983:321.
- Stenorrhypis** - Grolle, R. 1963:441; Jones, E.W. 1968b:565.
- Stictolejeunea** - Gradstein, S.R. 1985:195; Jones, E.W. 1976b:50.
- Strepsilejeunea* see under *Cheilolejeunea*

Symbiezidium - Gradstein, S.R. & van Beek, J. 1985:221.

Symphogyna - Grolle, R. 1980:330; Vanden Berghen, C. 1965:156.

Syzygiella - Jones, E.W. 1976b:48; Vána, J. 1985:81.

Taxilejeunea - Grolle 1974:93; Jones, E.W. 1967:289; 1976b:50.

Thysananthus - Vanden Berghen, C. 1950:35.

Tritomaria - Vána, J. 1982:78.

Tylimanthus - Jones, E.W. 1980:317.

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Gillet, H. & Jovet-Ast, S. 1957. Deux *Riccia* de l'Air (Territoire de Niger). *Rev. Bryol. Lichénol.* **26**:62-66.

Gradstein, S.R. 1975. A taxonomic monograph of the genus *Acrolejeunea* (Hepati-cae), with an arrangement of the genera of Ptychanthoideae. *Bryoph. Bibl.* **4**:1-216.

Gradstein, S.R. 1985. Contribution to a Monograph of the Lejeuneaceae, Subfamily Ptychanthoideae. *Beih. Nova Hedwigia* **80**:1-253.

Gradstein, S.R. & van Beek, J. 1985. A revision of the genus *Symbiezidium* Trevis. in Gradstein, S.R. 1985. Contribution to a Monograph of the Lejeuneaceae, Subfamily Ptychanthoideae. *Beih. Nova Hedwigia* **80**:221-253.

Gradstein, S.R. & Vanden Berghen, C. 1985. *Schiffneriolejeunea* sect. *Pappeanae* en Afrique. in Gradstein, S.R. 1985. Contribution to a Monograph of the Lejeuneaceae, Subfamily Ptychanthoideae. *Beih. Nova Hedwigia* **80**:173-

Grolle, R. 1960a. Nachtrag zur 'Revision der *Clasmatacolea*-Arten'. *Rev. Bryol. Lichénol.* **29**:68-91.

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Grolle, R. 1972. Zur Kenntnis der *Adelanthus*. *J. Hattori Bot. Lab.* **35**:325-370.

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APPENDIX IV: TECHNIQUES OF TAXONOMIC REVISIONS

Taxonomy is the basis of biology! Even in a period when systematics and taxonomy are regarded as secondary, it must be understood that taxonomic knowledge is necessary. No physiologists or molecular biologist can work without the circumscription of the species he is working on, no ecology is possible without the knowledge of the species living in an ecosystem. The necessary knowledge is obtained by taxonomic revisions and monographs. They differ in the intensity of work. Revisions are confined to a particular geographic area, to the necessary study of type material and in addition to representative material. Monographs are more detailed and deal (especially in smaller genera) with all available herbarium material.

Revisions and monographs have an enormous importance. Their results are needed to obtain the exact species number of a genus and they provide the necessary basis for a phytogeographical research.

Generally, much more species have been described than there really exist. This is the result of a) a narrow species concept, especially in the 19th century, when small modifications (e.g. in colour) were described as new species; b) theological reasons, since the evolution theory was not known or later not accepted in the 19th century and it was believed that God has created the species anew in every continent and every island; and c) the wide ranges of bryophytes, which the result that the same species was

collected in different parts e.g. in the neotropics during different expeditions e.g. in Brazil, Colombia, Bolivia and Mexico, and every time described as new. Later, bryologists had not the knowledge to revise the species worldwide but they were rather specialized on countries or continents (the French on Africa, the North Americans on South America) and a species could be known from both continents under two (or more) different names.

The rates of reduction are quite high, as seen from some examples in the Dicranaceae (see bottom page).

These reductions have also an effect on the rate of endemism, which is also decreasing, e.g. in the genus *Campylopus*.

The phytogeographical consequences of revisions are enormous, as shown by the distribution maps of species of *Microcampylopus* and *Campylopodium* before and after a revision. Therefore phytogeographical interpretations of unrevised genera must lead to fatal errors!

General introductions to taxonomy can be obtained from the existing textbooks (e.g. Stuessy 1990). Therefore the script is confined here to the techniques of taxonomic work, especially because there are no instructions available.

	Species described	Species accepted	Reduction %
<i>Pilopogon</i>	14	8	43
<i>Atractylocarpus</i>	19	9	53
<i>Microcampylopus</i>	27	3	89
<i>Campylopodium</i>	12	2	84
<i>Campylopus</i>			
Africa	256	50	81
Neotropics	320	65	80
Subantarctis	74	14	81

Percentage of endemic *Campylopus* species:

	Before Revision	After Revision	Flowering Plants
Hawaii	70	30	94
New Caledonia	50	0	90

Tab. IV.1: Numbers of species in genera and percentage of endemic species before and after taxonomic revisions.

1. Taxonomic revisions

Revisions are often said to be „old fashioned“ as they are mostly and primarily based on traditional methods. However, we have to realize that we are working with a group of organisms for which there is no well-founded estimate of the total number of species world-wide – due to the lack of generic revisions on a world-wide basis.

A major problem is the revisions of genera with high numbers of species. It is clear that mostly genera with relatively few species have been revised so far. Large genera are said to be time-consuming and difficult because of the large number of specimens one has to examine, copious literature and taxonomic data. Therefore it is said that revising a genus of 30-50 species seems to be impossible to do in a reasonable time, especially for students. However, this is a matter of *efficiency*.

Good revisions can easily be made by interested and motivated students, as is shown by many publications prepared even as teachers exam or master's theses. The main problem is that a lot of time will be wasted *if the work is not well organized*. With this in mind, instructions to using

taxonomic methods were published by Frahm (1989).

In the business world, each process is highly structured and wasted time is minimized. Taxonomic work can also be efficiently structured in much the same way. For that reason a working scheme has been derived for revisions prepared by students. This working scheme is proposed and explained here. It shows that taxonomic revisions can be prepared in a reasonable time with the highest efficiency and without delay caused by an incorrect organization of work.

There are principally two methods of preparing taxonomic treatments:

- (1) The specimen orientated method and
- (2) The type specimen orientated method.

The first method starts a study from zilch. All taxa already described are at first not considered; only specimens are examined and these are classified independently. After that, the taxa described are taken into account and compared with the results of the initial classification. Theoretically this seems to be the most independent way to produce a monograph or revision,

but it has practical disadvantages. It takes an enormous amount of time to obtain one's ideas of how to classify 3000 or 5000 specimens. All specimens from different herbaria must be continuously filed as new and sorted according to the developing ideas. Clearly, using this method requires a great deal of taxonomic experience, which a student usually does not have. Although this method is free without from predisposition and may give the best results in the end, I cannot recommend it for beginners.

The second method is the type- (or better the type specimen) orientated method. This concerns revisionary studies based primarily on the study of type material. All other specimens are compared with the species concept derived from the type specimens. This seems to be the easier of the two methods and it is also the more commonly used. It also gives results in a reasonable time and is recommended for students.

The following is an outline of a working scheme for mosses and consists of 12 steps as summarized in the figure.

1. Compile from *Index Muscorum* and its Supplements a list of accepted species, with synonyms on file cards or in a taxonomic file (text file or database).

2. Compose a list of all authors of taxa (see Sayre 1977 for the locations of herbaria). Then request to borrow the necessary type specimens (plus all additional material of that genus) from the herbaria. If you are a beginner and your name is not well-known (yet), it is advisable to have some words of recommendation from your supervisor or professor. The addresses can be obtained from „*Index Herbariorum*“, or, for bryophyte herbaria, from Vitt et al. (1985).

3. Look at the distribution data in the *Index Muscorum* to determine which additional herbaria should be taken into account in requesting to borrow further material.

4. While waiting to receive the requested loans, copies of the original descriptions (protologues) are ordered through the interlibrary system or

copied in the library. The information on the type material is extracted and added to the taxonomic file.

5. Additionally, all available literature from the important geographical ranges is examined.

6. All literature is compiled in a literature file.

7. When the borrowed herbarium specimens arrive, all types are studied first. They are examined and, if possible, permanent microscope slides are prepared. („If possible“ means that sometimes the type specimens are too scanty to allow deatching any part of it permanently; furthermore, some herbaria exclusively forbid detaching and removing any parts of type specimens.) All essential characters are illustrated or photographed and plates with figures are prepared for each type specimen. If necessary, nomenclatural problems are studied, as for instance lectotypifications.

8. The labels of the type specimens and all other specimens received on loan are copied and glued on file cards or the label information is typed into the computer (text or database). The file cards are arranged alphabetically. Notes can be added to the files or file cards during study.

9. All illustrations of the types are arranged for easy access, for example by pinning them up on the wall or a bulletin board. By comparing the illustrations, possible synonyms can be detected. These initial suspicions can be confirmed by comparing the permanent slides.

10. For the species remaining at this stage of the work, an identification key is prepared (again with the help of illustrations and slides). During this preparation, further synonyms may be detected.

11. Using this key, the non-type specimens from the herbaria are studied to determine whether they fit into the species concept derived from the types. In this manner, misidentified specimens can be revised, specimens belonging to other genera can be excluded, or specimens representing undescribed species can be found.

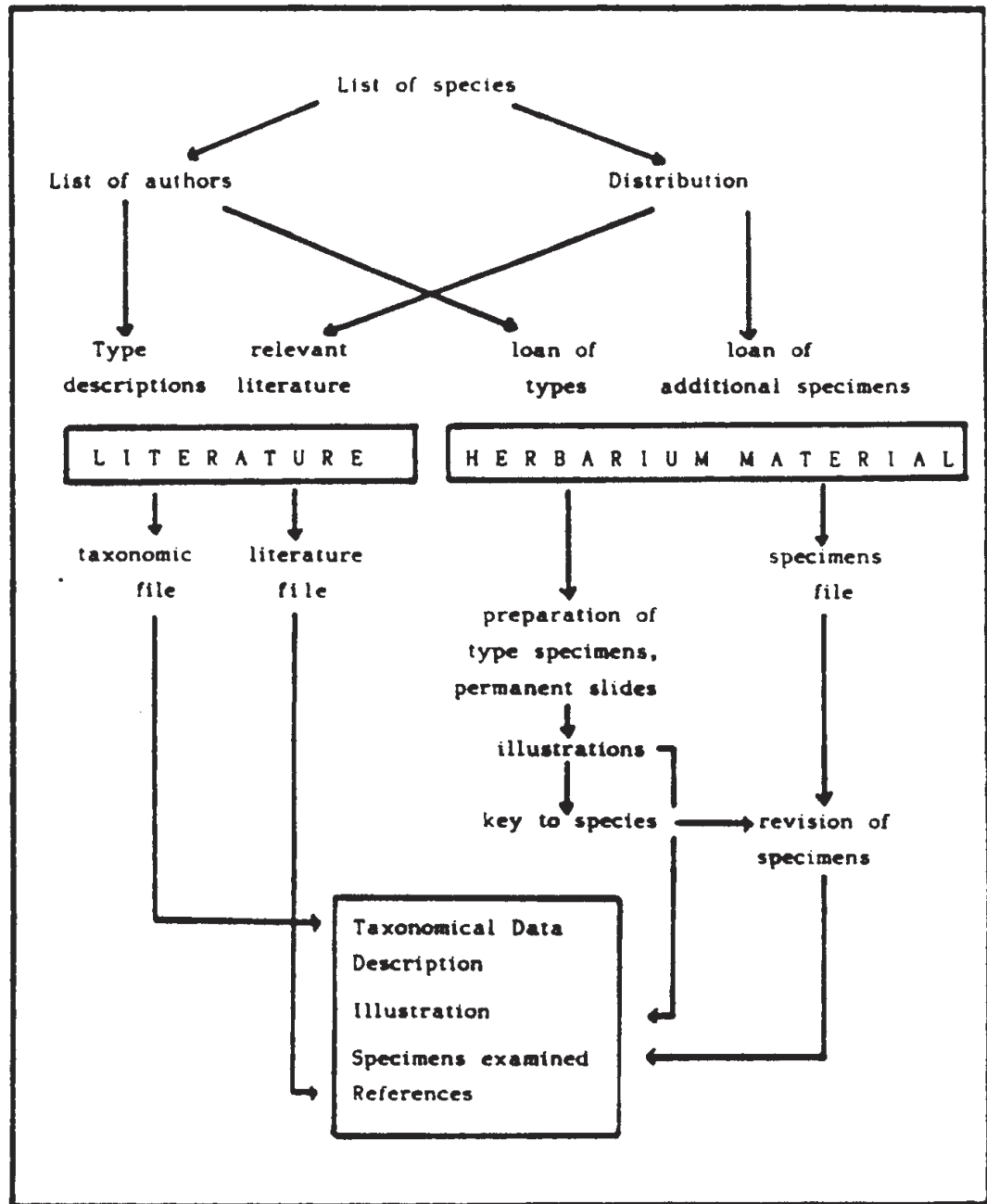


Fig. IV:1: Working Scheme for taxonomic revisions. From Frahm (1989).

12. In order to prepare the manuscript, the existing files and illustrations are simply merged together, and descriptions are added. If you are planning to publish the paper in a certain journal, you should take into account the journal's style and format.

A basic revision then consists of the following:

- a) taxonomic data of accepted species and synonyms (with taxa, citations, and type information) taken from the taxonomic file.
- b) descriptions: this is provided with the help of the illustrations, microscope slides, and examination of the herbarium specimens to cover the variation of characters. Special notes are taken from the comments on the specimen file.
- c) illustrations: this is taken in the case of several synonyms from the best or most typical one. If there is considerable character variation, at least some of it should be displayed in the illustrations.
- d) lists of specimens examined compiled from the specimen file, and
- e) references, compiled from the literature file.

Other methods used in taxonomy are biometrics, chemosystematics, cytology, cultures, SEM techniques, techniques for illustrations, and knowledge of nomenclatural rules, which are not dealt with here. The necessary knowledge can be obtained from the general literature because it is principally very similar to taxonomic work of other systematic groups, e.g. flowering plants. Phenetic and cladistic analyses are discussed in the next chapter.

Frahm, J.-P. 1989. Taxonomic methodology. *Bryol. Times* 89: 1-3.

Sayre, G. 1977. Authors of names of bryophytes and the location of their herbaria. *Bryologist* 60: 502-521.

Stuessy, T.F. 1990. Plant taxonomy. The systematic evaluation of comparative data. New York.

Vitt, D.H., Gradstein, S.R. & Iwatzuki, Z. 1985. Compendium of bryology. *Bryophyt. Biblioth.* 30: 1-335.

2. Phenetic and Cladistic analysis

Today, the classical revision is accomplished by either a phenetic or cladistic analysis, which makes the interrelationships between taxa more clear.

A. Phenetics

A phenetic analysis is based on morphological and anatomical characters. The resulting dendrogram reflects the „phenetic distance“, that means the affinities between taxa based on overall similarity.

In contrast to cladistic programs, no difference is made between apomorphic (derived) and plesiomorphic (primitive) character states. Therefore it is often argued that phenetic analysis show morphological similarity but not evolutionary trends; in other words, the groups achieved through a phenetic analyses are not natural, because they do not accurately reflect the evolutionary history (speciation) of the group.

In fact, the results of phenetic and cladistic analyses of a given group are often very similar. The reason is that similarities are often based on homologies and homologies have a common evolutionary origin. So similarity frequently can (but must not always) be based on common origin.

Phenetic analysis is performed with a cluster analysis. The data for a cluster analysis have to be prepared in a table form, in which species (in rows) and character states (in columns) are listed. (By the same way, species and relevées can be used in vegetation analysis)

The variables (character expressions) can be coded in several ways:

1. Sequentially. All characters are listed and numbered. The corresponding numbers are entried in the table.

2. Presence/absence. For every character state, the expression is coded as 0 or 1.

The results are the same regardless of the style of the table.

Next, the similarity of species 1 against species 2, 3, 4 and so on, are calculated, then 2 against 1, 3, 4, and so on, species 3 against 1,2,4,5, and so on. The similarity is calculated as percentage similarity, various Similarity Indices (Jaccard, Sørensen etc.), or Euclidean Distance. It is important to know that Euclidean Distance cannot be used for data matrices with 0 and 1.

Finally, the similarity indices are plotted against each other in a dendrogram. The axis shows the value of the similarity index. Most easily understandable is the percentage similarity. E.g., if two species have 9 of 10 characters in common, they are linked in the dendrogram on the 90% level.

This method has the advantage that it is absolutely objective and the resulting dendrogram illustrates very nicely the morphological similarity of the taxa.

Programs for cluster analysis

MVSP (Multivariate Statistical Analysis)

Written by W.L. Kovach. It includes several statistical methods such as correspondence analysis etc. The price is about £ 80. A shareware version can be tested free and can be obtained from the IAB software library by J.-P. Frahm. This version can only deal with up to 100 variables.

STATISTICA

A commercial Windows program, which includes many statistical features. Price about \$900.

B. Cladistics

A cladistic analysis shall „reconstruct phylogeny“. It is based on a similar data matrix as the phenetic analysis, but the resulting dendrogram does not show phenetic but „patristic“ distance, that means distance in evolutionary terms.

The cladistic method was founded by the German entomologist Willi Hennig, who worked in the USA. He wrote a textbook on „Phylogenetic

Systematics“ in German, which was translated by others into English. Later, the original German manuscript was published. It is different in some respects from the English translation. This first cladistic analyses were „hand made“ in contrast to later computer-assisted analyses.

The method is principally based on the assumption of apomorphic (derived) and plesiomorphic (primitive) characters states. Only groups defined by apomorphic character states are accepted, since only they are considered monophyletic, i.e. sharing the most recent common ancestor and including all descendants of that ancestor. Due to recognition of apomorphic and plesiomorphic characters states, the method is somewhat subjective, although there are principles to determine which characters are apomorphic and plesiomorphic, and therefore it is hypothetical (as also stated very strictly by Hennig). Later the computerized cladistic analysis was introduced as a „scientific“ approach to systematics.

For a better understanding of cladistic principles, performing a handmade cladistic analysis is strongly recommended.

List of Computer Programs for Cladistic Analysis

Most of the programs are today outdated, since these were DOS-programs which do not run anymore on an actual PC. The most commonly used program is PAUP. It was written for Apple computers and is accordingly easy to use. The Windows version is not as user friendly; it is more or less the DOS version running in a window. Therefore many labs, although they have Windows-PCs, have an Apple computer for running PAUP.

Hennig86 (Farris 1988)

A relatively simple but very effective program for finding most parsimonious trees with options for tree manipulating, successive weighting, and various free statistics. It is a mainframe program compiled for PC users. It runs under DOS and is relatively out of date concerning the use of

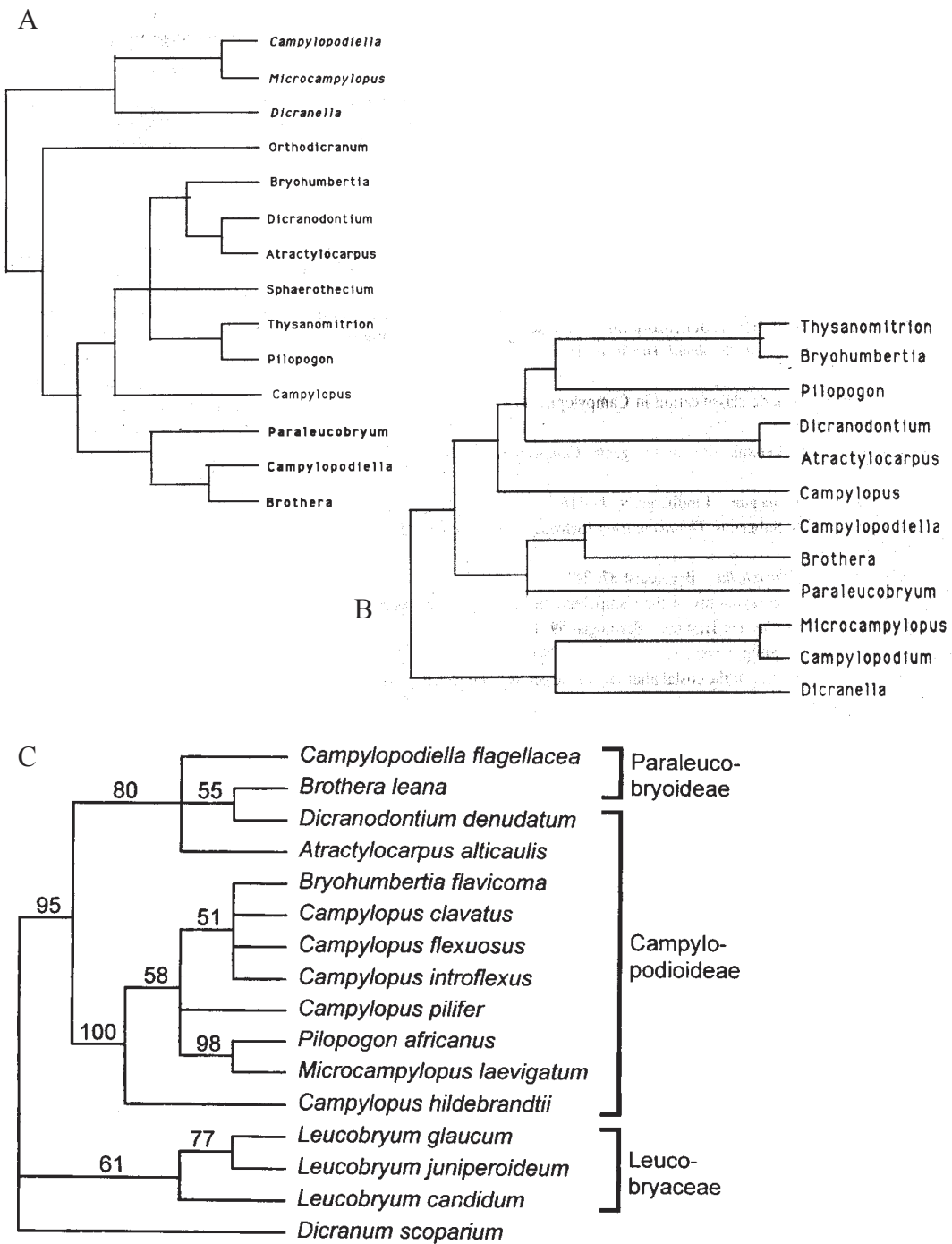


Fig. IV.1: Phenetic, cladistic and molecular analysis of the Campyloporioideae (Dicranaceae). A. Phenetic analysis (clusater analysis), B. Cladistic analysis using the program Treesearch, C. molecular analysis of cpDNA (ITS2), maximum parsimony analysis. A-B after Frahm, C. after Stech. All trees give different results, there is no truth in reconstructing relationships or phylogeny but different hypotheses.

memory capacity. The handling of the program is in the mainframe style and needs input of commands. The data have to be prepared with a text editor in a special way. The program is sold by the author, J.S. Farris, Swedish Museum of Natural History, S 10405 Stockholm. At least older versions have a non-graphical outprint. The compendium by Lipscomb (1994) is highly recommended as a supplement to the manual.

PAUP (Phylogenetic Analysis Using Parsimony)
An extensive program for finding most parsimonous trees with options for morphological and molecular data, tree statistics, bootstrapping, various consensus techniques etc. There is an earlier version for PC from 1985 and a much more extensive version for Macintosh from 1993. The old DOS version is not recommended. It needs a math-coprocessor to run. The program was written by D.L. Swofford and was distributed originally by the Illinois Natural History Survey at a price of \$50, but is now commercially distributed by Cambridge University Press at a higher price, also as a Windows version. The windows technique in the Mac and Windows version makes it easy to use and gives high quality outprints of the cladograms.

MacClade (Maddison & Maddison 1992).
This program does not generate cladistic analyses but allows to manipulate trees generated with other programs such as PAUP. Only available for Macintosh computers. It comes with an easy data matrix generator. Therefore it is recommended to use this program in conjunction with PAUP to generate data matrices and analysis of the trees generated by PAUP.

Phylip (Phylogenetic Interference Package)
This package contains a variety of phylogenetic programs for molecular and morphological data, inclusively maximum likelihood, parsimony and bootstrapping facilities. Versions for PC (DOS, not much recommended because of its difficult operation) and Macintosh. Phylip runs slower than PAUP or Hennig86, but is, however, available free of charge from the author J. Felsenstein, Dept. of Genetics SK-50, University of Seattle, Washington, Seattle, Washington 98195, USA.

COMPONENT Vers. 2.0, 1993
Written by Roderick M. Page as a Windows Version. It is comparable to MacClade and does not generate new trees but investigates and compares trees. Available from the Natural History Museum London at a price of about £ 80.

TREESEARCH (Bruggeman)
Written by the husband of Ida Bruggeman-Nannenga for her thesis. A DOS-Program which is relatively easily menu-operated. The data matrix must be prepared with a text editor. It has no real graphics output and is relatively slow but is available free. Copies can be obtained from the IAB software library and ordered from J.-P. Frahm.

Other programs:
CLINCH
ClADOS
NONAME and Pee-Wee

Of these programs, PAUP is recommended of the commercial and Treesearch of the public domain programs. The main problem with all problems is that they need a special data format. Therefore it is suggested to prepare own data by „overwriting“ existing files (e.g. the demo files) to avoid difficulties.

A serious problem and a funny exercise is to „feed“ different cladistic programs with the same data. The results will not at all be comparable!

Farris, J.S. 1983. The logical basis of phylogenetic analysis. In: N.I. Platnick & V.A. Funk (eds.), *Advances in Cladistics* 2: 7-36.

Platnick, N.I. 1987 An empirical comparison of microcomputer parsimony programs. *Cladistics* 3: 121-144.

Sober, E.R. 1983. Parsimony methods in systematics. In: N.I. Platnick & V.A. Funk (eds.) *Advances in Cladistics* 2: 37-47.

Wiley, E.G. 1981. *Phylogenetics*. J. Wiley & Sons, New York. 439 pp.

APPENDIX V: VEGETATION ANALYSIS (PHYTOSOCIOLOGICAL METHOD AFTER BRAUN-BLANQUET)

Vegetation analysis (in Europe unfortunately called „plant sociology“) studies the composition of plant communities. There are different approaches concerning the methods and results in North America and Europe. In North America, usually random plots are studied using statistical methods. In Europe, estimations of the cover of species are made within a selected plot. The reasons for the different methods are historical. When plant sociology was established in the 1920s, a hundred years long knowledge of the indicator values of the species existed and was common sense. So „typical“ species for a habitat were used to characterize plant communities. At that time, many universities in North America did not even exist, and there was no knowledge of the ecological indicator value of species before, on which studies could be based. In addition, North America is much larger and botanically much more diverse than Europe. Therefore a botanist from California could do nothing else than use statistical methods when he was working in Massachusetts.

In Europe there were originally different methods for plant sociology developed. In the boreal forests, the Finnish Hult and the Swedish Sernander estimated the cover of species by a scale of 10 units and classified plant communities by dominance of species, which was easy, since

the tree-, herb- and cryptogam layer of boreal forests is dominated by a few species. This method could, however, hardly be used in Central Europe. Therefore the swiss botanist Braun-Blanquet developed a method using a modified scale with 5 units and used *character species* and *differential species* for classification of vegetation units. Character species are typical of only one community (which is indicated by this species), and differential species are species which can be found in more than one vegetation units but differentiate a plant community from others in the surroundings. The study plots are not selected at random but they are chosen according to a principle. They must be typical, well-developed and homogenous. The so called Braun-Blanquet method was said not to work in the tropics. This is surely true for tropical forests, however, at the end of the 1970s it was successfully applied by Dutch botanists in the páramos of Colombia.

Bryophyte communities in the tropics were rarely studied in the past. Jovet-Ast (1949) was the first who studied epiphytic bryophyte communities in the French Antilles. Giacomini & Ciferi (1950) described a terrestrial bryophyte community from Venezuela with the Braun-Blanquet method. Petit & Simons (1974) described epiphytic bryophyte communities from Burundi. During the BRYOTROP project, studies of the epiphytic

bryophytes were originally made along the Peru transect with plastic sheets, which were wrapped around the trunks. The outlines of bryophyte cushions were marked with a pen and later the cover and combination of species were evaluated in the lab (Frahm 1987). However, this method failed in Borneo, since the bryophytes were too humid and water condensed below the plastic. Therefore the Braun-Blanquet method was used (Kürschner 1990) and proved to be very successful, since tropical bryophyte communities do not differ in their structure from temperate bryophyte communities. Later this method was used again in Central Africa (Kürschner 1995).

Frahm, J.-P. 1987. Struktur und Zusammensetzung der epiphytischen Moosvegetation in Regenwäldern NO-Perus. *Beih. Nova Hedwigia* 88: 115-141.

Giacomini, V. & Ciferri, R. 1950. Un'associazione crittogamica a *Polytrichadelphus* e *Cora* (*Coreto-Polytrichadelphum ciferrii*) su rocce della Foresta delle nebbie in Venezuela. *Atti Ist. Vot. Univ. Pavia, Ser. 5, 9*: 211-217.

Jovet-Ast, S. 1949. Les groupements des muscinées épiphytes aux Antilles françaises. *Revue Bryol. Lichénol.* 18, 3-4: 125-146.

Kürschner, H. 1990. Die epiphytischen Moosgesellschaften am Mt. Kinabalu (Nord Borneo, Sabah, Malaysia). *Nova Hedwigia* 51: 76-85.

Kürschner, H. 1995. Wissenschaftliche Ergebnisse der BRYOTROP Expedition nach Zaire und Rwanda 4. Epiphytische Moosgesellschaften im östlichen Kongobecken. *Nova Hedwigia* 61: 1-64.

Petit, E. & Symoens, F. 1974. Les bryophytes des bois artificiels de *Cupressus* et d'*Acacia* au Burundi. Analyse factorielle de la végétation bryophytique. *Bull. Jard. Bot. Nat. Belg.* 44: 219-247.

Pócs, T. 1978. Epiphyllous communities and their distribution in East Africa. *Bryophyt. Biblioth.* 13: 681-713.

Field practice

The methods described are here applied to the study of bryophyte communities. Several items such as phenology or stratification, which are only important for flowering plant communities, are omitted.

1. Selection of study plot

The study plot must be homogenous. Homogeneity can be determined with some experience from the aspect or by statistical methods, e.g. a line taxation or a frequency analysis.

The size can also be determined by experience. The right size determines whether all species of a community are included or not. If the area is too small, not all species are included. The size can be determined by a minimum area curve (species number per area curve). Species numbers are determined on a small scale (e.g. 5 x 5 cm), then the area is doubled and the species numbers are determined again, and so on. The species numbers per area are plotted on a graph. The minimum area is reached when the curve becomes a horizontal line, meaning the species number is not increasing anymore.

The size for bryophyte communities is between 5 x 5 cm (epiphyllous communities) and ca. 20 x 30 cm (epiphytic communities) or even considerably larger (terrestrial communities). It is adapted to the size of the substrate (leaf, branch, trunk). It needs not to be a square but can be a rectangle of any dimensions. The circumference of the study plot maybe marked with tape or wire.

2. Analysis

For each analysis, several parameters are noted:

- date
- description of the locality with exact indication of the location
- elevation
- subsequent number (or a combination letter/digit, e.g. A1, to indicate different analyses in different forests, different student groups etc.)
- size of the study plot (square centimeters or better length x width)
- exposition (use compass)

inclination (if no clinometer is available, a large protractor with a perpendicular can be used) total cover of bryophytes, eventually also that of lichens and phanerogams

special notes can be made concerning other factors, e.g. the height of the tree, the diameter of the trunk, the forest type, illumination, density of canopy etc.

all species within the study plot are listed, starting with the most dominant ones.

At least, the cover of a single species is determined or estimated. The Braun-Blanquet school uses the following index:

r (rare) a single plant

+ a few plants with a cover less than 1%

1 1-5%

2 5-25%

3 25-50%

4 50-75%

5 75-100%

The index 2 has proved to be insufficient, because many species have a cover between 5 and 25%. Therefore some authors divided it into 2a (5-15%) and 2b (15-25%).

The problem of this scale is that it is non-linear and cannot be used for computerized evaluations (e.g. a cluster analysis). In this case, the indices are converted later into means of the indices (e.g. 37,5 for 3). It is also possible (although not official Braun-Blanquet method) to use estimations of the percentage cover of each species, which can be directly processed in the computer.

The Braun-Blanquet method includes the indication of the „sociability“ of species, a scale of 5 units (1-5) to indicate whether the plants grow e.g. single, in groups or in mats. Since the sociability is regarded as part of the life form and thus species-specific, it is not recommended here and does not give very much additional information.

3. Tablework

All separate vegetation analyses are combined in a table (the „raw table“), today by means of a spreadsheet program. The table is then sorted

a) horizontally by arranging all species in the sequence according to their cover, e.g. the species with high cover at top,

b) vertically. This arrangement groups similar study plots together, e.g. separates different communities or divides a community in subunits (e.g. wet and dry expressions, expressions from vertical or inclined trees etc.). The table can also be arranged according to ecological parameters in the head of the table, e.g. pH of bark or soil, elevation, exposition etc.

For every species, the frequency (steadiness) can be calculated, that means how often it is represented in all analyses in %. The frequency is expressed in a scale from I-V:

I = 1-20%

II = 20-40%

III = 40-60%

IV = 60-80%

V = 80-100%

Based on this table, many statistical studies can be made to analyse the community according to homogeneity, community coefficients etc.

An easy way to show the interrelationships between the study plots is to proceed the data in a cluster analysis. The table is then reduced to a two-dimensional matrix of species and study plots with their values (variables). The resulting dendrogram shows the affinities between the study plots. For details of the cluster analysis, see the Taxonomy section of this paper.

4. Phytosociological systematics

Communities can be classified by

a) dominant species, that means the species with the highest cover. The species need, however, not be typical of a community, since they can be weedy species occurring in several communities (and thus having no indicator value),

b) differential species, that means species which differentiate a community from another one within a stand (e.g. forest). They cluster in the table in a block. This is the best way to classify communities in the tropics,

c) by character species. Character species are indicator species for certain narrow ecological

niches. They need not automatically have high frequencies. This requires, however, knowledge of the ecology of the species.

All other species are named „associates“. They have no indicator value or are part of the community by chance.

The name of the community is given by the name of the character species or differential species with the ending *-etum*, the species name in the genitive. If there is another species involved, it is added with the ending *-o*.

Examples (from BRYOTROP studies in Zaire):

Plagiochiletum terebrantis

Drepanolejeuneo - Microlejeuneetum africanae

Lejeuneo flavae - Plagiochiletum divergentis

The basic community is called association. As in the systematics of plants, subunits (comparable to subspecies) are made, here called subassociations. They are expressed with the name of the characteristic species with the ending *-etosum*, e.g. *Marchesionio excavatae - Plagiochiletum salvadoricae - Plagiochiletosum praemorsae*.

Several associations are grouped to unions (like species to genera), unions to orders and orders to classes. Orders have the ending *-ion*, orders *-etalia*, classes *-etea*.

APPENDIX VI: BRYOPHYTE CHECKLISTS OF TROPICAL COUNTRIES**A. Neotropics***Belize*

Whittemore, A.T., Allen, B. 1996. The liverworts and hornworts of Belize. *The Bryologist* 99: 64-67.

Bolivia

Hermann, F.J. 1976. Recopilacion de los musgos de Bolivia. *Bryologist* 79: 123-171.

Brazil

Yano, O. 1981. A checklist of Brazilian mosses. *J. Hattori Bot. Lab.* 50: 279-456.

Colombia

Churchill, S.P. 1989. Nuevo Catalogo de los Musgos de Colombia. *Tropical Bryology* 1: 95ff.

Churchill, S.P. & Linares, E.L. 1995. *Prodromus Bryologiae Novo-Granatensis*. 2 vols. Bogotá.

Churchill, S.P., Griffin III, D., Munoz, J. 2000. A checklist of the tropical Andean countries. *Ruizia* 17: 1-203.

Costa Rica

Bowers, F.D. 1974. The mosses reported from Costa Rica. *Bryologist* 77: 150-171.

Morales Z., M.I. 1991. Las Hepaticas comunicadas para Costa Rica *Tropical Bryology* 4: 25-58.

Ecuador

Steere, W.C. 1948. Contribution to the bryogeography of Ecuador I. A review of the species of Musci previously reported. *Bryologist* 51: 65-167.

Guianas

Florschütz-de Waard, J. 1990. A catalogue of the bryophytes of the Guianas. II. Musci. *Trop. Bryol.* 3: 89-104.

Gradstein, S.R. & Hekking, W.H.A. 1989. A catalogue of the bryophytes of the Guianas. I. Hepaticae and Anthocerotae. *J. Hattori Bot. Lab.* 66: 197-230.

Mexico

Bourell, M. 1992. A checklist of the bryophytes of Chiapas, Mexico. *Tropical Bryology* 6: 39-56.

Sharp, A.J., Crum, H.A., Eckel, P.M. (eds.) 1994. *The moss flora of Mexico*. 2 vols. New York Botanical Garden.

Panama

Stotler, R., Salazar Allen, N., Gradstein, S.R., McGuiness, W., Whittemore, A., Chung, C. 1998. A Checklist of the Hepatics and Anthocerotes of Panama. *Tropical Bryology* 15: 167 ff.

Paraguay

Buck, W.R. 1985. A preliminary list of the mosses of Paraguay. *Candollea* 40: 201-209.

Peru

Menzel, M 1992. Preliminary checklist of the mosses of Peru. *J. Hattori Bot. Lab.* 71: 175-254.

Venezuela

Moreno, E.J. 1992. Aproximación al conocimiento de las briofitas de Venezuela. *Trop. Bryol.* 6: 147-156.

Pursell, R.A. 1973. Un censo de los musgos de Venezuela. *Bryologist* 76: 473-500.

B. Tropical Africa

Born, S., Frahm, J.-P. & Pócs, T. 1993. Taxonomic Results of the BRYOTROP Expedition to Zaire and Rwanda 26. A new checklist of the mosses of Central Africa. *Tropical Bryology* 8: 223-274.

Kis, G. 1984. Checklist of the mosses of the south-east tropical Africa. , J. Vana (ed.): *Proceedings of the 3rd Meeting of the Bryologists from Central and East Europe.* Univ. Karlova, Prague.

Kis, G. 1985. Mosses of south-east tropical Africa. An annotated list with distributional data. 170 p. , Vacratot (Ungarn): Institute of Ecology and Botany of the Hungarian Academy of Sciences.

O'Shea, B. 1995. Checklist of the mosses of sub-Saharan Africa. *Tropical Bryology* 10: 91-198.

By the activities of the British Tropical Bryology working group, the checklists for Africa are available as downloads from the Internet.

Checklist of Malawi bryophytes

Checklist of mosses of sub-Saharan Africa

Checklist of liverworts of sub-Saharan Africa

C. Tropical SE Asiatic countries; Mosses

(by TIMO KOPONEN)

Areas (according to "Index muscorum") and countries of east and southeast Asia, and the Pacific, and their moss checklists.

As 2:*China*

Redfearn, P. L., Tan, B. C. & He, S. 1996: A newly updated and annotated checklist of Chinese mosses. *J. Hattori Bot. Lab.* 79: 163-357.

Jiangxi

Fang, Y.-M., Enroth, J. Piippo, S. & Koponen, T. 1998: The bryophytes in Jiangxi Province, China: An annotated Checklist. - *Hikobia*

Hunan

Rao, P.-C., Enroth, J., Piippo, S. & Koponen, T. 1997: The bryophytes of Hunan Province, China: An annotated checklist. - *Hikobia* 12: 181-203.

Hong Kong

Li, Z. & Lin, P.-C. 1997: A checklist of bryophytes from Hong Kong. - *J. Hattori Bot. Lab.* 81: 307-326.

Taiwan

Kuo, C.M. & Chiang, T.Y. 1987: Index to Taiwan mosses. - *Taiwania* 32: 119-207.

Japan

Iwatsuki, Z. 1991: Catalog of the mosses of Japan. - 182 pp. Hattori Botanical Laboratory, Nichinan.

Korea

Choe, D.M. & Choi, H.H. 1980: A list of bryophytes of Korea. - *Rep. Sci. Education* 12: 27-55.

Gao, C. & Chang, K. C. 1983: Bryophytes of North Korea. - *Misc. Bryol. Lichen.* 9: 163-170.

As 3:*Bangladesh*

O'Shea, B.J. 2003. An overview of the mosses of Bangladesh, with a revised checklist. *J. Hattori Bot. Lab.* 93: 259-272.

Bhutan

Long, D. G. 1994. Mosses of Bhutan II. A checklist of the mosses of Bhutan. - *J. Bryol.* 18:

339-364.

Burma (Myanmar)

Tan, B. C. & Iwatsuki, Z. 1993: A checklist of Indochinese mosses. - J. Hattori Bot. Lab. 74: 325-405.

Cambodia (Kampuchea)

Tan, B. C. & Iwatsuki, Z. 1993: A checklist of Indochinese mosses. - J. Hattori Bot. Lab. 74: 325-405.

India

Gangulee, H. C. 1969-1980: Mosses of eastern India and adjacent regions. 1-8. - Calcutta.

Laos

Tan, B. C. & Iwatsuki, Z. 1993: A checklist of Indochinese mosses. - J. Hattori Bot. Lab. 74: 325-405.

Nepal

Noguchi, Z. & Iwatsuki, Z. 1975: Musci. - In: Ohashi, H. (ed.) Flora of eastern Himalaya. Third report. - Bull. Univ. Mus. Univ. Tokyo 8: 206-242.

Pakistan

Nishimura, N. & Higuchi, M. 1993: Mosses from Pakistan. - In: Nakaïke, T. & Malik, S. (eds.), Cryptogamic flora of Pakistan 2: 275-299.

Townsend, C. C. 1993: New records and bibliography of the mosses of Pakistan. - J. Bryol. 17: 671-678.

Townsend, C. C. 1994: A small collection of mosses from Himalayan Pakistan. - J. Bryol. 18: 181-185.

Townsend, C. C. 1995: Further mosses from Himalayan Pakistan. - J. Bryol. 18: 811-814.

Sri Lanka

Abeywickrama, B. A. & Jansen, M. A. B. 1978. A check list of the mosses of Sri Lanka. - UNESCO - Man and Biosphere National Committee for Sri Lanka Publ. 2: 1-25.

Vietnam

Tan, B. C. & Iwatsuki, Z. 1993: A checklist of Indochinese mosses. - J. Hattori Bot. Lab. 325-405.

As 4:

Eddy, A. 1988, 1989, 1996: A handbook of Malaysian mosses. 1-3. - 1. Sphagnales to Dicranales. - 204 p. 1988; 2. Leucobryaceae to Buxbaumiaceae. - 256 p. 1989; 3. Splachnobryaceae to Leptostomataceae. - 277 p. 1996.

*Indonesia**Borneo*

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APPENDIX VII: PRINCIPLES OF PREPARING CHECKLISTS

by TIMO KOPONEN, SINIKKA PIIPPO, JOHANNES ENROTH, PENGCHENG RAO & YIN-MING FANG

While compiling the bryophyte checklists of the Hunan (Rao et al. 1997) and Jiangxi (Fang et al. 1998) Provinces of China we came across several difficulties. First, some of the records for Hunan and Jiangxi were mere lists of names without documentation, and second, some of the records are doubtful on the basis of the general known distribution of the taxa. Also, some records cited in earlier checklists were based on literature not available to us, or even on unpublished manuscripts. We feel it necessary to discuss the methodology of preparing checklists here.

Checklists are a useful tool of floristics and phytogeography and a summary of the flora of a certain area. The area dealt with may be a country, some smaller area such as a province, or, more rarely, a continent or some other larger geographical area. Examples of all of these can be cited and are listed by Lane (1978) and Greene & Harrington (1989). Basically, two different kinds of lists have been published. Some checklists are mere lists of the flora existing in the area dealt with, while some others carefully document all the knowledge by citing published records. The method and layout partly depend on the area dealt with. In many European countries, North America, and Japan the checklists may be mere lists without any further information. This is easily understood; for instance, it might be difficult to find a publisher

for a checklist including references to all published records of *Ceratodon purpureus* for Finland, while to cite the records of *Ceratodon* for Pakistan is still reasonable. Most useful checklists are those which give the reasons of the nomenclatural changes, list the synonymies, and cite the additions to the flora. This is done by citing the papers dealing with the nomenclature and floristic publications. Floristic publications cite, or their should cite, the specimen on which the record is based, and the museum or herbarium in which this voucher is being kept. Some checklists include floristic novelties, Grolle & Piippo (1984) being a good example of this. The discussion above leads to the first principle.

Principle 1

The basic principle of all checklists is that they should be based on herbarium specimens which can be traced and the identity of which can be checked, when or if necessary.

The basis of any checklist is the floras of the area dealt with, if such works exist. Fortunately, bryologists of earlier generations were careful in their documentation. Works such as Fleischer's (1904-1923) flora of Java, Brotherus' (1923) Fennoscandian flora, Bartram's (1939) Philippine flora, as well as some more modern floras (Gangulee's 1969-1977, Whittier 1976, Magill 1981, 1987, Allen 1994, Bai & Zhao 1997) cite specimens. This tradition should be continued

when the floras of imperfectly known areas are published. This can be done very shortly e.g. by citing the specimens from which the figures of the work were drawn, or by citing widely distributed exsiccata (e.g. Noguchi 1987-1994). We have found it most unfortunate that Eddy (1988-1996) did not continue this tradition.

The lack of documentation in flora works creates problems to checklist writers. How to deal with records which are highly doubtful on the basis of the general distribution of the taxon? Here is one example. Chang (1978), in her flora, published a description and an illustration of *Mnium venustum* (= *Plagiomnium venustum*) and cited it for many Chinese provinces. However, *P. venustum* is an endemic of the Pacific coast of North America; the illustration in Chang's flora does not represent it; and no Chinese specimens have been available for study (Koponen 1981, Koponen & Lou 1982). Redfearn et al. (1966) noted these references and did not accept *P. venustum* as reliably recorded for China.

Principle 2

Flora works lacking documentation should be used very critically as basis of checklists.

The records published in popularizing books, or in works dealing with forestry or describing vegetation, are often not documented. These records can be doubted on the basis of the general distribution of species, although all distributions are not yet known in detail. Checklists should not be based on unpublished manuscripts, undocumented mimeographed lists, or data files not readily accessible, either.

Principle 3

Popularizing books and plant sociological papers lacking documentation should be omitted or used very critically as basis of checklists. Records in unpublished manuscripts and data files not generally available should not be used as basis of checklists.

Well-documented checklists are useful sources of information and using them should not be time-consuming. The references to the literature should

be given directly in the list, and not as numerical code (compare Piippo 1990 and Redfearn et al. 1996). Miller et al. (1978) contains a vast body of knowledge of the floristics of the Pacific area. The distribution of taxa is readily available, but finding the references for a certain taxon within a certain group of islands is laborious. Nomenclatural and floristic additions can be cited in notes (e.g. Koponen et al. 1977, Corley et al. 1981).

Principle 4

Information in checklists should be given in a form easily available.

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APPENDIX VIII: METHODOLOGY OF RELEVÉE STUDIES

Bryology is not only collecting bryophytes. Although collecting was and is the main motive or even urge for many bryologists and the only stimulus for many amateur bryologists, it is just the necessary base for further scientific evaluations. In the begin of bryology, collecting was done for taxonomy (discovery and description of new species). At that time, species were collected like stamps in most complete sets. This period is over now. Although there is still a chance to detect new species in the tropics, this chance is small, requires much taxonomic knowledge and is something for specialists. The next step was to describe the distribution of known species. This has been done by many single floristic studies, in Europe also by systematic mapping of species. There is still a need for such floristic studies in the tropics, especially in undercollected areas, however, this can not be all. Therefore some instructions are given here to complete and intensify the bryological knowledge of tropical countries.

Usually, at random collecting makes scientifically not much sense and is something for hobby-bryologists. Important is to gather data. For the evaluation of data, a comparable base is required.

Base for such studies can be hectare plots (see appendix II) or trees for epiphyte studies.

Most important is that all parameters, especially the size of the study sites, are comparable. Comparisons of species numbers are only possible if based on the same area. There were publications comparing species numbers of national parks of very different size, in different altitudes and by collections from different periods (for one park even collections from 90 years ago included). The advantage of hectare plot studies is that the base for comparison is given. There are also examples in which the species numbers of trees are compared without regard to their size. Species numbers can only be compared for the same area, and this concerns also studies of epiphytes, where the calculation has to be based on for instance a square meter around the tree trunk.

1. **Calculation of *alpha diversity*** (species per area). For that purpose, the area (study plot, relevée) must have the same size and should have a minimum size to cover all species of a vegetation type. The minimum size can be determined by a *species-area curve*: with measuring tape, an area of 1 square meter is marked and all spe-

cies in this area are counted. It is not necessary that the species can be named but need only to be differentiated. Next, the side length is doubled to 2m (4 m²), then to 4, 16, 32 and 64 m (4096m²) and again all species are counted (or those in addition to the previous area). Finally, the species number is plotted against the area. The resulting curve shows at first a steep increase, but will get suddenly flat, when the species number is saturated and ends asymptotic. Minimum area is the area where the curves flattens.

2. After collecting and identifying the species, the data can be evaluated:

- by writing a species list by families
- by calculating the ratio hepatics (incl. hornworts) : mosses,
- by calculating the number of species by families and displaying the results in a bar chart or pie-chart.
- by calculating the number of species on different substrates (soil, rocks, rotten wood, epiphytic).

3. **Calculation of beta-diversity.** After the inventory of several relevées along an ecological gradient (see appendix II), the relevées can be compared. For the calculation, diversity indices such as the Sørensen Index can be used:

$$\frac{\text{Species common in both relevées}^2}{\text{Species number relevée A} + \text{B}}$$

The species numbers of different relevées can be visualized in a line chart.

4. **Determination of the mean annual temperature.** For altitudinal transects and comparison of relevées, the elevation is used as parameter. This has, however, important disadvantages:

- (a) The vegetation belts vary in altitude by latitude; they are higher situated in equatorial latitudes but decrease towards the poles.
- (b) The exposition varies the vegetation. At the same altitude, we may have different vegetation types on N- and S- exposed slopes. Therefore a N-exposed relevée in 2000 m cannot be compared with a S-exposed one at the same altitude.

(c) The vegetation belts differ in mountains of different altitude: they go higher up in large mountains but are lower in small mountains („Massenerhebungseffekt“).

The main ecological factor which shall be expressed by the altitude is the temperature., which decreases by 0.6-1°C per 100 m altitude. Instead of giving the altitude, it is possible to refer to the mean annual temperature. Usually, mean annual temperatures can only be determined by long series of temperature measurements, to cover the different temperatures in different seasons (seasonally climate). They can also be determined by the temperature of spring water (except thermal springs, of course), since the water has a constant temperature over the year. Measurements over a year are, however, not necessary in the inner tropics, where the daily fluctuations of the temperature are higher than the annual fluctuations (daily climate). The mean annual temperature is measured in the soil below 30 cm depth, where the influence of the day/night fluctuations are no more expressed. To determine the soil temperature in 30 cm depth, a solid metal stick of this length is required, which is bent 90° at the top. The stick is pushed into the soil to form a hole of 30 cm depth. In this hole, a thermometer is lowered. It can be a normal thermometer fixed by a cord or an electronic thermometer lowered by its cable. There are special electronic soil thermometer with stick-like electrode.

By this way, the mean annual temperature can be used as reference instead of the altitude.

5. **Determination of cover.** The cover of bryophytes varies much between lowland, montane and subalpine forests. It can easily be determined even without knowing any species but gives nevertheless good results for the determination of altitudinal zones, because bryophytes reflect best the different ecological conditions in different altitudes. The cover is estimated as average percentage on the ground and on trees. Determination of cover is different from that of species richness, since both factors are not correlated. A few certain species can form large masses. By this way, the species numbers can be sometimes higher in areas with low cover and vice versa. It is also recommended to differentiate between the cover of hepatics and mosses.

For epiphytes, the thickness of epiphyte cover can also be determined. In the lowlands, epiphytes are usually found only as crusts of liverworts, whereas in the subalpine forests high, thick masses of epiphytes cover trunks and branches. The measurements are taken with a ruler.

6. Determination of life forms. As expressed in chapter 5.1, the different life forms are direct expressions of different ecological conditions because they are adaptations to these conditions. The main life forms are determined:

- crusts: predominantly liverworts (*Lejeuneaceae*, certain *Frullania* and *Radula* species) creeping on bark of trees).
- cushions
- tufts (*Dicranum*, *Campylopus*-species)
- mats (most pleurocarps)
- wefts (*Lepidozia*, *Bazzania*, *Teleranea*)
- turfs (*Polytrichaceae*)
- fans (*Porotrichum*, some *Plagiochilas*)
- pendants (predominantly *Meteoriaceae*)

Some life forms listed here may not be found, others may be differentiated by themselves if it seems appropriate (e.g. creeping mats of *Macromitrium* or similar, dendroid turfs). For each life form, the percentage is noted.

7. Determination of phytomass. The amount of phytomass of bryophytes is not only an expression of the „mossiness“ of a habitat but determines the water storing capacity of the forest. In tropical forests, it concerns usually the phytomass of epiphytes due to the lack of larger amounts of bryophytes on other substrates (except of subalpine forests).

Some bryologists have determined the phytomass of a complete tree, which had to be cut for that purpose, and all bryophytes had to be removed, dried and weighted. This requires much effort and is not always possible. Therefore an alternative method has been developed based on measurements of the phytomass per square meter. For that purpose, one square meter is marked on a tree trunk. The trunk resembles a cylinder ($2\pi rh$). First the circumference of the trunk is measured with a measuring tape ($2\pi r$). Next the height of the cylinder is determined by dividing 1 square meter by the circumference. Example: If a tree has a circumference of 1 m, the height of the

cylinder is also 1 m and the cylinder has an area of 1 m². If the tree has a circumference of 50 cm, the height must be 2 m to give an area of 1 m². If the trees are too small that the length of the trunk area gets too long, or if the amount of bryophytes is too much that it will get difficult to handle, also half a square meter may be taken. All bryophytes are scratched off the trunk with a knife and collected in a bag. The material is air dried and the weight is determined by a balance. Any pieces of bark, litter, accompanying ferns, filmy ferns, other epiphytes or dirt has to be removed before. By this way, the phytomass may be determined on several representative trees and an average can be calculated. Statistics recommended the use of random trees, however, in this case the number of trees must be quite high. Often, the epiphytic cover on trees is very uniform and in this case, even the result of the determination of the phytomass of one representative tree comes the result of the determination of the phytomass of numerous trees chosen at random very close.

With some reservation, the phytomass of epiphytic bryophytes can be calculated for a hectare. First it is estimated how many times the open area on the trunk, where the material was scratched off, fits on the whole tree (say 12 times). Then the number of trees with a similar cover are counted in an area which can be overlooked (e.g. 20 x 20 m, say 5). This would mean that 60 times the weight of the phytomass per square meter is found on 20 x 20 m and approximately 25 times as much on a hectare. This estimation gives a rough idea of the phytomass per hectare and may not be interpreted too exact. It is only an approximation but gives an idea whether there are 20 kg or a ton of bryophytes to be expected on a hectare.

8. Determination of water storing capacity.

From the dry weight of bryophytes per square meter, the amount of water can be determined which is stored in the bryophytes. For that purpose, the whole mass of bryophytes taken from one m² is soaked in water. Water is now stored within the bryophytes as well as between the bryophytes. The latter, the so called interception water, is difficult to determine. If one tries to put the bryophytes on a balance, the interception

water will run off. Therefore the surplus water is carefully shaken off and the wet bryophytes are weighted. The experience shows that the bryophytes normally store water between 2,5 and 3,5 of their dry weight. An exception are samples from lowland forests with much Leucobryaceae and Calymperaceae, which store more (5x). Roughly, the dry weight may be multiplied by three to get the water storing capacity. The same can be done with the hectare values.

9. Determination of pH of substrates. Species composition is generally much influenced by the pH of the substrate, but not as important in the wet tropics. The higher the precipitation, the lower is the influence of the substrate. All measurements of barks of trees in the tropics revealed acidic conditions, ranging between 4 and 6, which can, however, be different on different host trees and therefore explain different species composition (beside bark texture and chemistry). Bark pH is measured by cutting off small pieces of the outermost bark, filling them in a 50 ml plastic bottle and adding 2.5 times as much distilled water. The bottles can be shaken and measured immediately or kept for 24 hours and measured then. Important is, that always the same methods is used (same amount of bark, water, time). Measurements are taken with an electronic pH-meter. If the pH-meter is new or has not been used for a longer time, it is important (a) to soak the electrode in water (no distilled water!) before and to calibrate it with two buffers. The electrode has to be stored all the time between the measurements in water. Recommended are electrodes which are sealed or filled with gel which need not to be refilled. There are special flat head electrodes for direct measurements on bark. It is also the only way to measure the pH of bare rock. The surface of a plane piece of bark (which can be removed from the tree for that purpose) or a plane part of a rock is covered with distilled water and the electrode is pressed upon it. There must be direct contact with water between surface and electrode.

Soil samples are treated in the same way: soil is filled in a plastic bottle and diluted with 2.5 times of distilled water. The treatment (shaking or not, leaving it for short or longer time before the measurement) has only a small influence on the

result (+/- 0.2 values).

10. Determination of light intensity. Light intensity, humidity and temperature depend on permanent fluctuation. Therefore single measurements cannot be taken into account. An exception is the relative light intensity. It indicates the percentage of light in an habitat, e.g. different parts of the forest floor, as compared to the light in the open. Therefore the relative light intensity of e.g. 5% can be determined at any time of the day or during cloudy or sunny weather.

Although the intensity of certain wavelengths relevant for photosynthesis (PAR) is measured for physiological purposes, the cheaper lux meter with a sensibility for a different light spectrum can be used to characterize different light and dark habitats.

Measurements are taken with the light sensor exposed to the sky in different parts of a forest. Instead of making numerous at random readings, it is recommended to measure the lightest and the darkest spot which are inhabited by bryophytes to get the span of light intensity in a forest stand. Alternatively, the light can be measured for habitats of different species to get the photophilous and skiotolerant species differentiated. Shortly before or afterwards, the light is measured in the open (on a road, clearing, spot of a fallen tree, open trail). The reading from the open is divided by the values received in the forest to get the percentage light. Complications arise only if there are wandering clouds. In this case attention has to be paid that the measurements have only been made at moments with open sky. Equally mats of clouds are not a problem.

11. Determination of relative humidity and temperature. For these factors, momentary measurements make rarely sense. Only if data loggers are not available, measurements in minimal hours intervals can provide daily curves of both factors. For both purposes, electronic devices are recommended.

Humidity was originally measured with psychrometers. These were two thermometers, of which one had a „sock“ covering the bulb. The sock was wetted with water, causing a decrease of temperature by evaporation. The lower the air humidity the higher was the evaporation and the

higher the difference between the „dry“ and the „wet“ thermometer. The relative humidity (rh) could then be interpolated from a table. It is still possible to prepare two thermometers in such a way for that purpose as the cheapest way of a psychrometer. Only the table is required, which can be copied from ecology textbooks. Later, electronic psychrometers could calculate the value, but were still operating with two thermometers. Some time ago, a substance has been discovered which changed the resistance of electricity in dry and wet state. Therefore simple modified micro-voltmeter could be used for measuring humidity with this new electrode similar to an electronic thermometer.

Long term measurements of temperature and humidity are possible with data loggers. Such instruments were extremely costly and large in the past but as all electronic equipment got small and cheap within the time. Recent dataloggers have the size of a credit card or a match box. The latter cost less than 130\$ and can store up to 1700 readings in any interval. They are connected to a computer to initialize and download the data, which are displayed in curves and can be exported to MS Excel.

Humidity data loggers give an idea how long the bryophytes are in wet state in different habitats. Bryophytes are poicilohydric and therefore metabolic active only when turgescient. So they do not suffer from any temperature or humidity in dry state (which is called anabiosis). Important is, how long they can be photosynthetic active in different habitats. For that purpose, there must be sufficient light and an air humidity above 80%. Below 80% rH, the bryophytes dry up (some hygrophytes even sooner). Since phytomass is a direct result of net photosynthesis, the „mossiness“ of an area is a result of photosynthetic active phases (except for lowland forests with high rates of respiration) which can be determined by a datalogger.

12. Determination of life strategies and propagation methods. This answers the question, how is the bryoflora composed, of species which are sterile, or propagate vegetatively and are thus less flexible against destruction or disturbance and are candidates to get likely locally extinct by human impact or by fertile species which easily

propagate over wide distances? An analysis of the life strategies already gives rough results. Also a calculation of the mode and frequency of vegetative or sexual propagation. Detailed analyses how the species propagate (by gemmae, tubers, fragments, leaves, or sexually by spores, how large are the spores, how long are they presumably distributed, can be helpful.

APPENDIX IX: THE USE OF COMPUTERS IN THE FIELD

Computers got irreplaceable tools for scientific work, also for the fieldwork. They can be used for normal computer work as well as devices for measuring instruments or for navigation. Many computer work can already done in the field and many time can be saved by using the computer during fieldtrips. There are, however, limitations. The computer must be portable, and therefore only notebooks, handheld PCs or Pocket PCs are in question.

1. **Notebooks** do almost everything a desktop computer can do, but have lower size and weight. They can be synchronized with desktop computers and by this way all current projects and files can be carried around. The main restriction is still, that the batteries last only 2-3 hrs. Therefore a use abroad is very much confined if the notebook cannot be recharged, except for the use in fieldstations. On trips by car, the notebook can be recharged from the car battery. Necessary is a special 12V charging cable (usually for this special notebook and thus expensive). An alternative is the use of a 12V – 110/220V converter. This converter allows to use all electric devices in the car (up to an limit of 100 – 400 W depending on the model), including electric shaver, charger for cell phones, batteries for measuring instruments, cameras and video

cameras. It has to be observed that the converter has enough watt. For instance, if the notebook charger has 220V and 1,8A, it needs 400 W. This can easily be calculated by Ohm's formula.

Possible applications for notebooks in the field are wordprocessing, use of spreadsheets (e.g. for data from ecological measurements of light, temperature, humidity etc.), use of databases e.g. for collecting information, download of data from data loggers and navigation.

Navigation is possible by connecting a GPS to the notebook. It requires special software such as FUGAWI (see internet). If maps are loaded into the computer, the position is indicated. This facilitates travels in the tropics, showing always the own position. The software also allows to calibrate scanned maps or aerial photographs. By that way, also maps of a national park or the study site of a field station can be used. By walking through a study site, the exact position is indicated and even single trees can be located and marked in the map. Beside, notebooks allow access to the internet (webpages, e-mails) through the cell phone in areas which are covered by cell phone networks. Else the use of satellite cell phones is possible (which is, however, expensive).

So called subnotebooks are smaller (A5 size) but also run with normal computer systems and have similar limitations concerning battery life. The battery life is limited by use for the screen, for the hard disk and a CD ROM.

2. Handheld and Pocket PCs differ from notebooks in their size (pocket format) and the feature that they have all programs and data in RAM, which costs hardly any electric power. They have no power consuming disk drives and most of the energy is used to illuminate the small screen. By this way, they last 10-40 hrs. Some older models use 1,5V batteries, which can easily be exchanged and no charging is required. Handhelds have a tiny keyboard and are easier to use for data input, Pocket PCs are used with a small pointer. There are 3 different systems of such small PCs: Palm, Psion and Windows CE. They all require that the handheld or pocket PCs are connected with a desktop computer or notebook from which programs or data can be downloaded. The programs on the small computers are different from the large PCs and the files must be converted. Nevertheless, these small computers allow the use of Word, Excel, Filemaker or Access files in the field. Accessing the internet is equally possible by a cell phone which is connected by cable or IR device. By the same connection, sending of SMS messages or even pictures taken with a digital camera is possible if the camera uses flashcards and the Pocket PC has a flash card slot (not in Palmtops). They can also be used for downloads of data logger data (much easier than with the heavy notebook), e.g. Orion dataloggers with Palm handhelds (special connecting cable required). They can also be used for navigation using the right software and by connecting the GPS to the handheld (special cable required). So much of the work such as writing notes, drafts of manuscripts, collecting data, measurement data can already be done in the field. The PC can be worn in a pocket, has a weight of 150 – 300 g and can be used up to 40 hrs without recharging.

APPENDIX X: PHOTOGRAPHING IN THE FIELD

Photographing during collecting trip and projects in the field is a nice way to illustrate the results for publications and presentations (posters, lectures). For bryologists, knowledge of as well as equipment for close up photography is required. So far, photographing was mainly done with single lens reflex cameras. For close up photography, special equipment such as close up lenses, macro objectives, extension tubes, bellows, special flash lights (ring or macro flashes) and tripods were needed, a proper storage inclusive, which could sum up to several kilograms which had to be carried around.. The films had to be developed, framed, and today usually digitised for Powerpoint presentations, beamer slide shows or incorporation in reports or publications.

Today, digital cameras allow to get digital pictures directly; they are much smaller and have a lower weight, can be carried around in a pocket, some need not close up equipment, have a built-in flash, are much easier to use, cost less than a SLR equipment, have a monitor on which the pictures can be controlled, and bad pictures can be erased and cost no money. They are highly recommend and therefore photographing with classical cameras is no more treated here. The disadvantage that they are sensitive to high humidity is shared with 99% of all SLR cameras, which are also operated electronically (there are only very few manual cameras left).

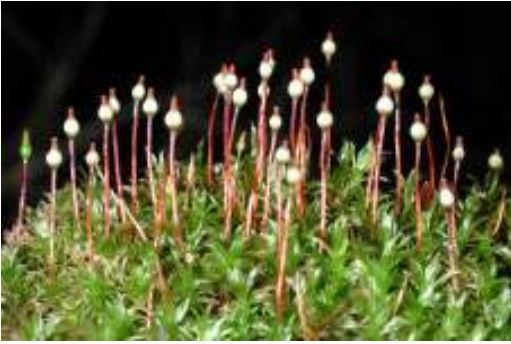
Of course, not all digital cameras can be used for our purposes. Not as important is the resolution. All cameras with 2 megapixels and more are sufficient. The latter allows prints of half letter size in photo quality. In opposite, too high resolution causes too large picture files. Important is, that they have

- a shortest distance of 1-4 cm (many have only 20 or 40 cm),
- high ASA (can be varied up to 800, even 1600 ASA) to allow pictures in the dark understorey of forests (many have only 100 ASA),
- good optics (digital cameras of optical companies have better optics than those of computer companies such as Epson etc.)
- possibility to shut off the flash
- possibility to over- or underexposure the picture
- possibility for spot measurement
- possibility to shift the focus/exposure
- a common storing device such as a compact flash card.
- a filter screw at the objective
- zoom without elongating the objective.

So all digital snapshot cameras are excluded. Among the remaining cameras, there is a recommendation for Nikon Coolpix (900, 950, 990, 4500) cameras. These have developed to „cult cameras“ amongst biologists. The cameras allow a shortest distance of 2 cm, giving a picture size of 12 x 17 mm. If this is not enough, a handlens can be mounted before the objective

(a 10x handlens gives pictures of 5x7 mm size). Most attractive is the use of a 10x lightlens. The objective can be turned around in all directions, allowing pictures in difficult positions without laying in the mud or even from below (a fern leaf). The camera has all possibilities of the Nikon SLR cameras such as time or focus automatic, shift of exposure/focus, spot matrix measurement, over and under exposure etc. The built in flash can be used for close ups (from model 990 on, it can be directed to the object by a fingertip). These cameras can also easily be used at the microscope. There are expensive microscope adapter available, but an ocular, in which the 28 mm screw of the objective is drilled, does the same. The monitor can be turned 90° and allows a control of the picture when sitting before the microscope. Unfortunately, the newest models all have a built in battery and no exchangeable batteries anymore, which was easier to use in the field.

In general, the highest compression of the picture file can be used, which results in a size of 500 kb with a resolution of 3 megapixels. A compact flash card of 48 BM stores thus about 100 pictures.



A



B



C



D



E



F

Fig. X.1: Examples of bryophyte pictures taken in the field with a pocket size digital camera (Nikon Coolpix 990) without any close up accessories. A. *Tayloria magellanica*, B. *Hypopterygium arbuscula*, C. *Chorisodontium aciphyllum*, D. *Schistochila* spec., E. *Symphyogyna* spec., F. *Bartramia* sp.

APPENDIX 11: A GUIDE TO COLLECTING BRYOPHYTES IN THE TROPICS

by

Brian O'Shea*

1. Introduction

This guide is intended for any individual or group going to collect bryophytes in the tropics. Experience has shown that general purpose expeditions are often not successful in making useful collections of bryophytes: often only the commonest and most conspicuous specimens are collected. *Octoblepharum albidum* was called 'missionary moss' by the eminent bryologist H.N. Dixon because of the frequency with which it was collected by the inexperienced, and all the 'bryophytes' of one university expedition proved to be lichens. Even experienced bryologists from temperate regions do not always make good collections unless they are prepared to expend effort in familiarising themselves with the tropical flora before they go. This guide is produced with the intention of providing the necessary guidance to maximise the scientific value of tropical collecting expeditions.

There is a strong feeling against collecting amongst conservation-minded botanists, perhaps because historically there has been a 'stamp collecting' mentality amongst botanists. They

often saw their herbaria as collections of 'one of everything', rather than as reference collections which could be used to assist in future identification, in distributional studies, or for taxonomic studies. Some plants, including bryophytes, have been collected out of existence in the UK, and it is said that there is more material of some very rare plants in herbaria than there is in the wild. The UK flora is very well known, and is thus particularly susceptible to such threats.

In the tropics, the position is rather different. Very few areas are well enough known to be able to predict where rare or endangered bryophytes are to be found and thus deliberate over-collecting is unlikely to be a problem. Over collecting is also not a problem in areas that are endangered by external threats to the environment, such as dams or logging, and indeed for some collecting, for instance for chemical analyses, quite significant quantities may be needed. In most areas of the tropics, so little collecting has been done that almost any collecting is likely to be useful. The exception is the main tourist areas at locations such as Luquillo Mountains (Puerto Rico), Kilimanjaro (Kenya) and Kinabalu (Sabah) which have been quite well documented so that there will be little benefit in the non-expert making collections.

* Reprint from British Bryological Society Special Volume 3, 1989, with permission of the author.

(Permits are also required for collecting in such places.)

But why is collecting bryophytes from the tropics important? There are two main reasons. The first is the pursuit of scientific knowledge, which should need no explanation or justification to anyone going on a scientific expedition. The majority of the world's bryophytes exist in the tropics, yet they remain the least known. There is often a problem in identifying plants from the tropics because of the poor state of tropical bryophyte taxonomy (and the lack of relevant literature - see later). Consequently attempts to understand tropical ecology are limited because of the problems of being certain about what plant is being studied. In many tropical environments, bryophytes form a significant part of the flora, but the study of their ecology is restricted to the few who can actually identify them. As most tropical ecologists are not bryologists, this diminishes the relevance of their work. The more information we can get about bryophytes, the more it will be possible to help those attempting a synthesis of knowledge about the tropics.

The second reason is one of survival. About a third of all tropical forest has been felled or degraded already, and the rate is being maintained at about 20 to 40 hectares per minute. Most of this disappearing forest is botanically unknown, and thus potentially important information about specific plants, and also more general information of relevance to other areas, has gone without trace. Bryophytes are important in two major ways. Firstly, they have specific properties that make them important as the source of various chemical products of great potential value to mankind. This has been known for some time about flowering plants, but increasingly it is becoming clear that bryophytes also possess a number of biologically-active substances, such as anti-carcinogenic compounds, anti-microbial substances etc. and that the greatest variety of these occur in tropical climates (see Ando and Matsuo (1984) for a summary of these and other uses). The better understanding we have of the floristics of these plants, the easier it will be to exploit knowledge of bryophyte biochemistry. Secondly,

bryophytes appear to play a vital rôle in nutrient cycling and buffering in forests, as well as in water relations. Evidence about this is only just emerging, and this knowledge can only be gained by field investigation and the information derived from collecting.

This guide does not cover the planning or equipping of an expedition in any detail, only how to go about preparing for your trip and what to do when you get there to make sure your collecting trip is worthwhile for both you and science. The tropics may be an exotic place for you, but it is part of everyday life to the people who live there, so your attitude to them is important. Show your care and concern for both the local people and their environment to make your trip truly worthwhile.

If you have any comments on the material in the guide, please let the author know, and also get in touch if you have any queries - we have no intention of providing an expedition planning service, but we may be able to point you to the information you need.

2. Preparation

2.1 *The tropics* In deciding to make a trip to the tropics, you should already have a good idea about what you can expect to find when you get there, but you should make sure you have seen such publications as Richards (1975), Jacobs (1981), Longman and Jenik (1987) or Whitmore (1984) for tropical forests, Walter (1971) for the non-forested tropics, and Myers (1984) or Caulfield (1985) for the tropics in general, and Pócs (1982) and Richards (1984) for bryophyte habitats. For more specific information about a particular country or area see Davis et al (1986), and Greene and Harrington (1989) for available bryological literature.

2.2 *Planning* There are several excellent books and booklets about planning an expedition (which also contain pointers to more specialised books), so this is not covered here in any detail. Examples are Gifford (1983), Blashford-Snell and Ballantyne (1977), and the publications of the Royal Geographical Society's

Expedition Advisory Centre (EAC), such as Chapman (1988). Anyone planning a trip should contact the EAC at 1 Kensington Gore, London SW7 2AR (01-581 2057). Two short papers (Mori and Holm-Nielson, 1981; Delgadillo, 1987) on botanical/bryological trips to the tropics, although aimed primarily at professional botanists, are nevertheless of great value to any collecting trip in looking at both opportunities and constraints. Books on backpacking and 'travelling on a shoe-string' will also be useful if you are not well-financed (e.g. Lonely Planet Guides, Moon Guides, Frommer 'Dollarwise' guides). Hatt (1985) is a cheap and useful general book about travelling in the tropics.

Research the trip thoroughly, and know what to expect in the tropics in general, and in your target country (geography, language, customs, currency, weather etc.). Make sure all participants are taking it seriously and are similarly prepared, work out costs in detail and allow a generous contingency, find out what clothing is appropriate, consider medical requirements, get injections organised well in advance, organise your visas and discover what limitations there are likely to be on tourists. Work out the logistics of travel (how to get about with your team and equipment) making any bookings before you go if you can - it may take days arranging a trip across country when you are there. If you need to hire porters or guides, make sure you know how to go about doing this and how much the going rate is. This is likely to be much more successful if it is arranged locally for you, so a contact in the area is very useful. This will also help you over local laws, especially about collecting and travelling in remote or conservation areas. It should also alert you to any particular dangers including insects, snakes and other animal life, guerrilla activity etc. - be aware of the dangers and know how to deal with them, but don't panic.

Accommodation should be arranged before you go. Using tents or 'dormobile' type vehicles gives flexibility, but makes it less easy to get specimens dried. Missionaries are usually very welcoming, and it may be possible to use a mission as a base, or just for a night or two.

If the weather is seasonal and you can choose a time of year, go shortly after the rainy season, when the bryophytes will be at their best.

You may find throughout your trip that dealings with officialdom are eased if you travel as a tourist rather than as a scientific expedition.

The Embassy or Tourist Bureau of your destination country should also be able to provide information, as might specialist travel agencies - but all this should be found in more general guides such as those mentioned at the start of this section.

If you can, talk to your local experts about which bryophyte groups or geographical areas need particular attention - this may provide a focus for your expedition. Try the local bryological society (the BBS in the UK - address on the front page of this guide) (O'Shea, 1985), or the local herbarium (see below). The wet tropics, rich in both quantity and variety of bryophytes, may appear the most attractive area to visit, but drier areas are much less well-worked, and the plants are different and of interest because less well-known.

2.3 Overseas contacts, invitations and collecting permits The most valuable source of assistance in making your trip worthwhile is likely to be a contact in the area you are visiting - but you must be able to demonstrate the seriousness of your intent before somebody who doesn't know you will make any effort to help. This means amongst other things having someone concentrating almost solely on bryophytes, and that person being able to demonstrate some expertise. If you do not already have a contact, you could try looking in the International Association of Bryologists' Compendium (Vitt, Gradstein and Iwatsuki, 1985), which lists bryologists and herbaria in most countries in the tropics, or write to the Botany Department at the University nearest to your destination. You will find that an offer to collect for a tropical herbarium can be used to solicit a written invitation from that country, which is almost essential for fund raising. You may not even be allowed to collect if there is no

local collaboration. A local contact will also advise where collecting permits are essential (National Parks, Nature Reserves, etc.).

Many South American countries nowadays require you to have a permit (to be obtained via a local herbarium) for collecting anywhere in the country. Moreover, part of each collection needs to be deposited in a local herbarium. Some local herbaria may require you to deposit labelled specimens before you leave the country. It is obviously essential to be aware of such rules before embarking on a collecting trip in these countries. See Delgadillo (1987) for more details.

2.4 Funding The Directory of Grant-Making Trusts (published by the Charities Aid Foundation) and Grants Register (Macmillan) are very useful, but take a lot of going through and result in a huge amount of letter writing - most of which is likely to be fruitless. The EAC have a small booklet listing the most useful sources of funds, and private companies are also worth trying.

2.5 Maps It is useful to have good large-scale maps, and Stanford's (12-14 Long Acre, London WC2E 9LP) is the best source. They also stock a wide range of travel guides. Map libraries are also useful, such as that at the Royal Geographical Society (RGS). Look also at geological maps. This will give some idea of which areas might be promising to visit.

2.6 Expedition reports Writing up your expedition is essential. It is a good idea to look at a range of expedition reports to see what others have done, as not only will they give you an idea of what is required, but they may give you guidance on how other expeditions have prepared themselves. Botanical Gardens such as Kew or Edinburgh will have these, as does the library of the RGS/EAC.

2.7 Herbaria/libraries It is important to visit a bryophyte herbarium before a tropical trip, to survey relevant literature and to look at specimens from the region to be visited. These are usually part of the „lower plants“ or

„cryptogamic“ herbarium at the British Museum (Natural History) in London, Edinburgh Botanical Garden, the National Museum of Wales at Cardiff, or possibly at a local museum or herbarium. Telephone beforehand to make sure that it is convenient to visit, and that there is someone there to show you where things are (and for local museums, to check that they have appropriate tropical collections/literature). Their experienced staff will be able to provide advice and information on many parts of the world. It can also be very useful to visit herbaria while you are in the tropics, and indeed may sometimes be obligatory (see 2.3 above).

2.8 Types of expeditions Two-person trips are probably best, organised specifically to meet bryological needs. However, it is sometimes useful to join a larger, interdisciplinary expedition (e.g. a Royal Society expedition) where you may be relieved of some or all of the organisation. This may involve some compromising on areas to be visited, which may not include the best ones for bryology.

3. How much do you need to know about bryophytes ?

This document does not tell you how to distinguish bryophytes from other plants: if you are unfamiliar with bryophytes, you are probably not yet ready for a tropical collecting trip. Collecting bryophytes in the tropics will be much more profitable if you are already familiar with your local plants, particularly with the range of variation that can be expected, so that you know what distinguishes one bryophyte taxon from another. If your trip is still some time away, and you have time to get to know bryophytes before you go, first of all look at the standard texts: Watson (1981) and Smith (1978) in the UK, and also Schofield (1985) for a more general account. If this doesn't put you off (it takes some time to become familiar with even the common ones amongst the thousand or so taxa in the UK - so think of the problems of coping with a flora that could be even larger) attend some meetings of your local bryological society (O'Shea, 1985) or find a local bryologist who will help you. You

should certainly be able to distinguish between the main bryophyte groups, such as acrocarpous and pleurocarpous mosses, the Metzgeriales, Jungermanniales and Marchantiales in the hepatics, and the hornworts, as well as having examined some of the commoner tropical bryophytes. Usually the large and conspicuous plants are well-known; the dull and the inconspicuous may ultimately be more profitable. Even a little knowledge will make a big difference to your effectiveness, but I must emphasise that **your collection will be significantly more useful if you are already familiar with bryophytes, and no expedition should set with the main object of studying bryophytes unless its members already have some reasonable knowledge of bryophytes.**

4. Where to look

Most mosses and liverworts prefer moist, shaded places, although there are a few species restricted to deserts and other dry habitats. Normally, however, the moister the situation, the greater is the development of the bryophyte population, and in tropical areas they may compose the greatest part of the visible vegetation. Wherever clouds and moist winds strike mountainsides through the greater part of the year, the forest may be so overgrown and draped with mosses that the trees can hardly be seen, and a tree trunk may actually be only half its apparent diameter. In other forests (particularly lowland forest), the degree of shade may be sufficient to severely inhibit bryophyte growth, with most of the flora being in the forest canopy. If you are visiting a drier area (see also para. 2.1) choose the wet season to visit. Generally, providing there is enough light, the warmth and wetness provide good conditions for bryophytes throughout the tropics. The ecology of tropical bryophytes is covered well in Pócs (1982) and Richards (1984).

It is worth considering four main tropical substrates in more detail: water, trees, soil and rock.

4.1 *Water* In general, lowland tropical streams and rivers are not rich in bryophytes,

although they are a somewhat neglected habitat, and there are interesting (and probably new) taxa to be found, as well as a few plants that are confined to these habitats. A rather more interesting flora is found in mountain streams. In running water bryophytes will always be attached to rocks, tree roots or the stream bed, but some will almost always be submerged, whilst others will only occasionally be submerged. In standing water, a few liverworts may be found floating free, and there is often an interesting ephemeral flora around fluctuating ponds, growing on bare mud. Although some bryophytes can tolerate brackish conditions or occasional salt spray, the coast is not usually a productive area, although a few bryophytes usually can be found on old mangrove trees.

4.2 *Trees* Probably no trip to the tropics will omit the forest habitat, but cultivated land is also productive because of the greater light, and also because the trees are more accessible.

On trees in dense forests, the height above the base of the tree at which particular species of bryophytes grow depends on light and humidity. Light intensity increases from the ground upwards, but relative humidity decreases (and wind movement also increases), so that inside a forest, bryophytes such as *Frullania* and *Macromitrium* spp. which require good light and are tolerant of low humidities, are found mainly in the tree canopy. On isolated trees in clearings, parks, savannas, orchards etc., the canopy species grow much lower down, often nearly to ground level. A rich bryophyte flora can often be found near the ground for instance on old cocoa trees in plantations, but these are often fairly common species. Different kinds of tree have different bryophyte floras, although the species of tree is probably less important than such things as bark acidity and chemistry, and on the quality of the bark as a substrate: smooth and flaky bark will usually have a poorer flora than rough bark. When collecting bryophytes from trees, a sharp knife is essential, and a scrap of bark in the packet may add to its scientific value, (although there are simply too many tree taxa to be able to identify them from pieces of bark). Fallen branches and twigs should always

be examined, as should fallen trees - it may be the only way of seeing what grows at the top of the tree, unless you have tree climbing apparatus (see below). Trees are perhaps the most complex of bryophyte habitats in the tropics, because the base, different levels of the trunk, the crotches, the branches and the twigs may all have different species.

In addition, in a moist forest, many bryophytes are epiphyllous (growing on leaves), and the leaves of small trees and shrubs will be covered with bryophytes - mostly small liverworts - as will buttresses, if there is enough light. You will usually have to collect whole leaves in this case, as it is easier to collect a leaf rather than trying to scrape the epiphylls from the leaf surface. It is also best to collect whole twigs where these are covered with pendulous bryophytes, despite the problems they bring in fitting them into a herbarium. See the paragraphs on collecting for further details.

In dense forest, much of the forest life exists in the canopy. There are now several books describing the „enchanted canopy“ (e.g. Mitchell, 1986; Perry, 1986), and Perry in particular spends some time describing in outline the mechanics of getting into the canopy and moving about in it, but this requires a set of skills and equipment that you may not have with you. However, several bryologists have managed to climb trees successfully and safely (e.g. ter Steege and Cornelissen, 1988), usually by using a bow to shoot a light cord over a high branch, and then hauling up a climbing rope. The rope is then climbed using „ascenders“, which is hard work and takes a long time, but is safe and straightforward provided you have someone with you who has climbing experience and is familiar with ropes, slings, karabiners and ascenders. Where conservation is not important (see para. 1) it may be easier to have trees felled to get to the canopy bryophytes. In general, however, fallen branches and recently felled trees will be sufficient.

It is not safe to climb trees if you are alone, whether to collect bryophytes or to see where you are.

Lowland forests have always been assumed to have a rather small bryophyte flora, in contrast to the variety of phanerogams, but recent evidence suggests that lowland forests, particularly canopies are much richer than previously thought. Montane forests (especially ‘cloud’ or ‘elfin’ forests) are, though, much richer in both variety and quantity.

4.3 Soil Bryophytes growing on soil are particularly important in seasonally wet habitats in climates with dry seasons, such as savanna etc., especially on banks of streams. They show the same intolerance of variation in environment as bryophytes on trees, and the resulting narrow selection of habitat is characteristic of these plants. Some species will be more or less restricted to heavy, water-holding clays, whereas others are always on sand or gravel. Whether the soil is acidic or basic is extremely important to bryophytes, and as this may be characteristic for a species, it is necessary to be able to recognise this either by testing or through knowledge of the rest of the flora. Prior research on the geology of the area will help. The amount of moisture available at one season or throughout the year, the amount of shade or sunlight, and whether the ground is flat or inclined are all factors which determine directly the species of mosses and liverworts which occupy any habitat. An excellent illustration of this intolerance is that we can expect, and find, totally different moss populations in open clay fields and on deeply shaded clay banks in a ravine. The clay is the same, but the other environmental factors are radically different.

In open clay fields, dried up ponds or on mud flats along rivers, very small mosses, thalloid liverworts and hornworts may be found which are often overlooked, and could thus be very interesting. Old termite mounds are a good habitat for some bryophytes, such as *Fissidens* and *Dicranella* species. Man-made habitats are worth examining.

Within lowland forests, bryophytes rarely grow on the ground. Where there is exposed ground it is often acid, even on basic rocks. The type of soil which most markedly affects the

bryophyte flora is the white sand found in Amazonia, the Guianas, Borneo etc., which has a different flora from the usual clayey red or yellow lateritic soils. Another factor is altitude: there are more bryophytes on banks of trails and roadside cuttings at higher elevations.

4.4 Rock A single large rock may form the home for a dozen different bryophytes. Just as on trees, those at the base will be moisture loving, and those on top will be less so, depending on the exposure of the rock. The relative amount of light will have a large effect, so different sides of an isolated rock will have different amounts of bryophytes as well as different species. As with soils, the composition of the rock is extremely important, and alkaline rocks such as limestone will support an entirely different population from acidic rocks such as granite or quartzite. Be prepared to look for very small species, particularly of liverworts; you will need a knife to scrape these from the rocks. The ceilings and walls of caves into which daylight enters should also be examined.

Look as well at man-made habitats, not only where natural rock is used, but also on brick (particularly on the mortar) and concrete. Culverts may combine dampness and decaying concrete, so may have interesting species growing in them.

Without doubt, the most significant factor affecting bryophyte growth is the amount of moisture available. Mosses growing on tree trunks well above the ground or on exposed rocks will depend almost entirely on rain, dew or fog for whatever moisture they obtain. Consequently they must be types that tolerate a level of drought. Most of them can reduce their evaporating area and at the same time protect the growing point of the plant by the rolling or curving in of the leaves when they begin to dry. When the plants are moistened, even after many years of drought (for instance in your moss packet), the leaves swell, become green and spread out again. Practical advantage of this can be taken in two ways when collecting: firstly, moistening these bryophytes often results in a very rapid uncurling which aids identification;

secondly, during and after rain, the drought-resistant bryophytes become green and conspicuous: mosses suddenly appear prominently on rocks, walls and trees which previously seemed free of them.

Light can be limiting in lowland tropical moist forest, where only about 2% of the light at the canopy reaches the forest floor. It is also important in its relation to evaporation, and bryophytes in bright places are likely to be drought-resistant, unless growing in permanently damp or wet places. Although some live in very low light intensities (e.g. in caves), light is still necessary for photosynthesis.

Altitude is an important factor in determining the distribution of bryophytes as well as other plants, as you can see as you ascend a mountain. In the tropics, bryophytes are always more abundant and varied in mountainous areas, particularly above 1000m-1500m, and in the 'mossy' forests (2000m-2500m). The effect of altitude is complex, and includes amongst others: changes in humidity, more rapid radiation of heat, decrease in average temperature, decrease in atmospheric pressure, and increase in ultraviolet radiation. Depending on the physiology of particular plants one or more of these factors will apply more decisively in controlling distribution. Many mosses of high, exposed places are tinged with red, purple or brown.

5. How to collect

A simple rule for collecting is to assume that if two plants look different they are different; it is better to collect one species several times than to pass over a related species entirely - and the range of variation may in itself be a very valuable addition to a herbarium. Some species grow intermingled, especially liverworts, and are difficult or impossible to distinguish with a hand lens. It is also the case that bryophytes often have very strict ecological and habitat preferences, and apparently similar plants in different habitats may well be different species. So use your instinct and rely on a plant's „look“

- a distillation of all of its characteristics: colour, size, manner of growth, shape of leaf, branching, habitat and so on. You will notice that experienced bryologists usually have a good idea what a plant is before they look through their hand lens - and part of this skill is purely observational, based on a knowledge of variation amongst bryophyte taxa. Once you have „got your eye in“ you will find this an invaluable skill.

In temperate climates, most bryophytes that produce sporophytes do so in spring or late summer to autumn, but in more equable tropical climates sporophytes can be seen throughout the year, although each species has its own season. Sporophytes are often useful or even essential for identification, and they should therefore be searched for and collected, notably in the Meteoriaceae, which fruit very sparingly, so any fruiting stems should be picked out and packeted separately. Nevertheless, do not neglect to collect a specimen merely because you cannot see a sporophyte. The type of male and female sex organs is sometimes crucial for identification, so look for these also.

You should also make sure you collect the whole plant. Many tropical epiphytic mosses have conspicuous, pendant secondary stems, and inconspicuous primary stems running along the bark. The latter may be vital for identification of the material.

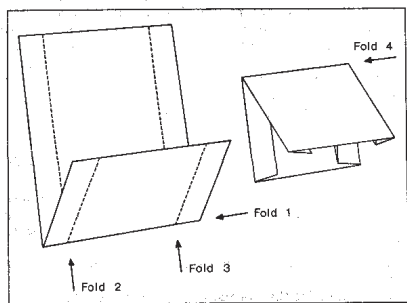
Some parts of the identification process are easier with fresh material, so even if you don't know the identity of a plant, it will still be useful to look for sporophytes or perianths in the field. With hepatics, it may be essential to look for oil bodies and to measure, count and describe them before they disappear on drying. This of course presumes the availability of a microscope in the field. (Sometimes the local herbarium, field station or botanical laboratory may be able to provide a microscope.) If you do this, keep the shoot that was studied separate in a small packet within the main packet. (This will guard against the problems associated with a mixed collection.)

Having found your bryophyte, there is no one way to deal with it - different collectors favour different methods. It is necessary first to collect and packet it in some way and to record collection information, then dry it (and keep it dry) before packing it to take away. This topic is covered from a professional herbarium viewpoint in Fosberg and Sacht (1965)

5.1 Equipment The most important items of collecting equipment are a hand lens, a knife a pencil or waterproof marker, and packets. The hand lens ideally should have a magnification of x20 with a fairly wide field of view, but this may not admit enough light in forests, so also take a x10 or x12. (You may find in a moist forest that your lens is of little use, being constantly misted up.) Always have your lenses tied round your neck. Even then it is possible to lose them, so take a spare (as it may be impossible to buy another one locally). The knife should be sharp and is needed for scraping off or digging up your specimen; it may also be required to cut off pieces of bark, and scrape the surface of soft rock. For entering virgin forest a machete (large knife) may be needed, unless you go with a guide. These can usually be bought locally very cheaply.

5.2 Packeting. Supplies of paper for packets is a very important detail, which should not be left to chance. One way is to packet your collections in envelopes made on the spot from local newspapers, collection data being written on the envelope in water-insoluble ink. Unfortunately, newspapers can be difficult to obtain in some countries, and expensive to buy, and in this case it may be much better to take thin paper along, such as old computer paper. Strong brown paper bags (as used for vegetables) are another option, but not if the bryophytes are wet and the gum holding the bags together is water-soluble. If the mosses are very wet, gently compress them to remove most of the water, and pack in double or treble thickness packets. This method is described in use in Cameroun by Edwards (1986). Wet paper will disintegrate if not handled carefully, so carry wet packets with care in the field and try to dry them as soon as possible, or transfer the bryophytes to dry

packets at the end of the day. The packets should be about 12cm x 8cm (about the size of 3in x 5in index cards), and can be folded as follows:



Any particularly small specimens should be wrapped in an appropriately sized piece of paper before being put in a normal size packet. This also applies to sporophytes or fertile parts of plants where these are in short supply, and have been isolated in the field - but always keep them attached to part of the gametophyte to avoid later confusion.

Earlier collectors used cloth bags (10cm x 20cm), with collection data written on the outside in black lead pencil or indelible pencil, or on a slip of paper inside. A dozen or so of the smaller bags are then put into a larger cloth sack, such as a 10 kilo flour or sugar sack, but this would now probably be regarded as unacceptable because the collections would get badly mixed. The tendency now is to packet species separately as much as possible. This can however be time consuming, and perhaps also difficult and inconvenient if the weather or light is bad, but is probably easier in the field when the material is still fresh than when jumbled together in the packet later. Generally, though, it is best to maximise your collecting time, and sort and document your specimens at the end of the day. You must use your common sense - after reading this guide you should be able to recognise good practice, so you must balance expediency with the scientific value of your collection.

Some bryophytes growing on soil are only very loosely attached to the substrate, for example in marshy areas, but others may be very closely adhering, and can only be removed with a piece of soil. As the collection dries, this will turn into dust, and produce a fine powder to decorate your herbarium whenever you open the packet. The plants are apt to break up if separated too roughly from fresh soil, so one strategy is to wash off excess soil gently at the earliest opportunity - although this may well also wash away any gemmae etc. if the washing is too vigorous. It is probably best to pare away as much surplus earth as possible from beneath the crust without breaking up the specimen, and packet in stiff paper, possibly using double packeting. Avoid bending the packet, but press lightly. Liverwort thalli in particular are prone to break into bits when the crust on which they are growing cracks. Try to avoid the use of plastic bags for collecting, as: they make it difficult to get the specimens dry; species can get very mixed up over a period of time; plants are likely to go mouldy or etiolated; they are more difficult to label properly. Plastic bags are acceptable only if you are going to transfer the specimens to paper packets within 24 hours, but this is not always easy to do if you have collected a lot, or if the weather slows down the processing of your day's specimens. Plastic bags are likely to be less of a problem in the cool mountains than in the hot lowlands - but they may force ripe hepatic sporophytes to shoot within a day. One circumstance where you will need to use plastic is if you are bringing live bryophytes back home, although you are likely to need a permit for this. You should use very sturdy bags, not the thin sort that tend to stick to the plant. Remove most of the moisture from the plants (squeeze them out) and there must be some air in the bag. Keep them as cool as possible e.g. by using a hotel room refrigerator, and reduce the time kept in plastic, for instance by collecting them the day before departure.

5.3 *How much to collect.* This can be an emotive issue. In the past, large quantities were collected, but today's more conservation-minded approach suggests that you should collect more modest quantities - enough to fill a 12cm x 8cm packet should be plenty for one collection. (This packet size is only approximate - choose a size that fits the way you wish to store them.) However, you may find that you will need more than one collection of a specimen, for:

- your own herbarium
- the local herbarium, so they have samples of everything that you collect (in some countries this may be a prerequisite of any collecting trip, for instance in Brazil, but is in any case an essential courtesy)
- if you need to send the plant to an expert for identification, it is courteous to allow him to keep part or all of the specimen
- you may wish to have specimens to exchange with other bryologists (this is a recognised practice in botany - herbaria and collectors frequently swap specimens to help build up representative collections)
 - a national herbarium

Sometimes it may only be possible to collect a small specimen, but remember that your collection won't be much use as a specimen if there is insufficient material to allow identification. Particularly for hepatics there are reasons why your collection should be more than just a few scraps:

- there may be a need to search a large amount of material in order to find the rare inflorescence, or the perfect peristome, or to get a feel for the amount of intracolonial variation - often very important with hepatics.
- the really important plant in a collection may not be what the collector saw, but some minute plant mixed with it. For a taxonomist working with such a collection it is maddening to have two stems of a possible new species, which are insufficient for adequate diagnosis. Similarly, what the collector thought was one species may be two or three that are difficult to distinguish, and what appeared to be an adequate

specimen may prove to be inadequate. This happens even with experienced collectors, for instance with the liverwort families Plagiochilaceae and Lejeuneaceae.

- if a plant is in any way unusual, it may be important to distribute samples to a much wider audience.

Nevertheless, even if you need five or six collections, do not over collect, in respect of the privilege of being allowed to collect, and in deference to the importance of the tropics in the ecology of the world. It is saddening to see torn tufts of moss hanging from trees and rocks following the depredations of the careless and wanton collector.

5.4 *Labelling* First of all, each packet should be uniquely identified, clearly and indelibly. Most collectors use sequential numbers for this. Many just start with collection number 1 and keep going, and this is perhaps the simplest and least confusing way. Others elaborate this slightly by adding a date or a site (e.g. 8806/1 or 880601/1 or site1/1 or a combination such as 88/site1/1) and so on, but it is important whatever method is used that mistakes in numbering do not occur - and mistakes are easy when writing hurriedly and in bad conditions, and especially when different nationalities are involved in the expedition. Pre-printed collecting notebooks with tear-off labels make it easy to maintain the sequence accurately. The numbering scheme should also be versatile - you may have to add extra numbers later (for instance where one mixed collection yields several specimens). The ink from ball-point pens is liable to fade in the tropics, so use ordinary or indelible pencil or waterproof markers.

In field conditions, numbering sequences are not always easy to maintain (you may accidentally use the same number twice, for instance, or forget the last number you used), and you may in any case prefer to sort out packet numbering at the end of the day. In this case, temporary field numbers are best, such as taking the date and time from a watch and writing this on the packet, so that there is no chance of getting the

packets out of sequence. (Incidentally, even supposedly waterproof watches seem to leak in the wet tropics, and it is best to use a fairly cheap watch in a polythene bag with silica gel crystals.) Another method is to use pre-numbered tickets, such as cloakroom tickets or menu pads, with the top copy going in the packet, the duplicate remaining as a record. It is also possible to write on many living phanerogam leaves with a ball-point pen or marker, for instance when collecting epiphylls.

If it is necessary to collect as much as possible in a limited time, you can put all specimens (packeted) from one habitat at one site in a bag together, and label the bag - but this method is obviously error prone.

It will also be necessary to record the details needed for the final herbarium packet, where these are not constant for the site, or for the day, e.g. substrate (rotting log, rock etc.) and identity, even if only known to family level (this saves a lot of time later). The type of rock, soil or tree is also very important, if you can identify, or describe it. For epiphytic specimens, indicate the precise location on the host (e.g. height on a trunk, side of a branch) and the host species if known; for epiphylls, indicate the host species (again, if known, although this is often impossible), which side of the leaf, and so on. Deep or light shade could be added, colour when fresh (specimens may turn brown on drying). This information can be written directly on the packet, or preferably in a notebook, or better still spoken into a dictaphone, which is quicker but needs transcribing to a notebook at the end of the day; tapes should be kept as a back-up in case of loss/soaking of the field notebook. Remember spare tapes and batteries, and also Murphy's law - if a piece of equipment can go wrong, it will. If you don't have a dictaphone (or if it is affected by the humidity, or goes wrong), it is less tedious to write directly on the packet, and only use the notebook for less frequent notes, such as when you arrive at a new site or habitat, but this is also more risky as paper packets can disintegrate. If you make field identifications, always check them again at the end of the day, when you are under less pressure

and have access to identification manuals. As it gets dark about 18.00hrs in the tropics, much packeting and documentation has to be done by artificial light. It is worthwhile taking a good lamp.

The general rule should be to document each specimen as fully as the collector is able. A few well-documented specimens may be much more useful than a mass of poorly documented ones.

Keep a notebook throughout your trip, and keep it up to date daily. If you are recording written data in the field, it is a good idea to use a different notebook in the field, as this may get wet or lost, and transfer data to your formal notebook at the end of each day. Provided it is not lost, the field notebook also provides a useful back-up to the formal notebook. This should contain details of all the places you visit - description, latitude and longitude or other map reference, altitude (**take an altimeter**) and so on, followed by the collection numbers for each site and habitat. You will need this information to write out the final packets, but also so that you can produce lists for the sites you visit and write an account of your trip.

Notebooks containing waterproof paper are available from Hawkins and Manwaring, Westborough, Newark, Notts.

Make sure you have enough information to write (as a minimum) the following on a label:

- collection number
- date
- identification (even if only to a broad grouping)
- locality - description, latitude/longitude or grid reference
- habitat - aspect, substrate, vegetation type
- altitude (if possible)
- other observations - associated plants, whether fruiting, abundance or rarity etc.

In some places you may only have a large-scale map (if any), and it is then very desirable to draw detailed sketch maps of collecting locations, together with measured distances to landscape

features. The description of each location should be sufficiently detailed that it can be refound, if necessary.

5.5 Drying Drying is essential, otherwise fungi will attack your collections. If you are in a dry area, it should be possible to air dry them over a few days (either spread in a single layer in the sun, or in your tent or room), but in a wet area, this may be a major problem and preoccupation. For those with an unlimited budget see Croat (1979) - take a pick-up truck with you, equipped with a professional herbarium drier heated by butane. More practical is some arrangement such as described in Frahm and Gradstein (1986), using a metal frame holding a wire mesh shelf, surrounded by a cotton curtain, and heated from below by one or two kerosene stoves. The apparatus weighs about 2.5 kg, but it is essential to have a reliable method of drying your specimens, otherwise, as Frahm and Gradstein point out, your specimens may become of more interest to a mycologist. (Do not use the strong heat used for vascular plants, unless you hang the bryophytes above the frame. 'Cooking' bryophytes will distort cell structures, preventing reconstitution on re-wetting and use in later growth studies.) Another alternative is to use net shopping or vegetable bags, hung up over heaters or on a line in the sun. Don't use a heavy plant press, as this can damage sporophytes and some critical morphological features of the specimen, although leaves with epiphylls should be pressed lightly when drying to keep them flat, as should very large 'hanging' moss (Meteoriaceae etc.). Use dry paper in this process, such as botanical drying paper, or thick wads of newspaper, and change daily until dry and don't mix with bulky flowering plants. The most comfortable method, especially in the humid tropics, is to hire an air-conditioned hotel room - your specimens, if laid out in a single layer, should be dry within 24 hours.

Delicate hepatics in particular will blacken with collapse of tissue if they are not dried carefully, and cells that have collapsed in this way do not recover when soaked. This can be a real difficulty with epiphylls, when the phanerogam leaf dries slowly, and prevents the hepatic from drying. A thin press, mentioned above, is the

only solution. Gentle pressing can also be an advantage with some thallose hepatics, but heavy pressing and roasting can make it impossible to recover the original cross-section.

In summary, dry as quickly as possible, at as low a temperature as possible.

5.6 Keeping them dry When specimens are thoroughly dried, they should be placed carefully in polythene bags to prevent them from picking up moisture from the air again. It is a good idea to bundle packets together with elastic bands (about 10-12 per bundle) for ease of handling. Greene (1986) recommends adding activated crystals of silica gel to the plastic bags, which are brought into the field in cotton bags, dried with the specimens and then put in one or two paper packets at the top of each bag. This also makes sure that any moisture that might get into the bag due to incomplete sealing or drying will be adsorbed by the crystals and not the bryophytes. Mothballs are equally useful. Sturdy bags should be used to provide protection during transport. The bags should be sealed tightly with sticky tape. Keep a close watch on the sealed bags, and open immediately any showing condensation, and re-dry the packets. A little dichlorobenzene amongst the packets will deter cockroaches and other pests, if the collection is to be stored for some time. Always pack the notebook separately from the specimens.

5.7 Packing for transport The physical volume of bryophytes that you collect may be surprisingly large, and you should think about how you are going to get them home before you start collecting. The stages will be:

- pack them carefully (see 'Keeping them dry' above) and tightly to avoid shaking about during transport.
- be able to carry them to wherever they are to be despatched from (which means if you are backpacking you may need to make periodic trips back to a post office).
- make arrangements to pack them properly - preferably in wooden crates (such as tea chests) that do not allow the plastic bags to be

damaged, or in strong cardboard boxes, preferably with strengthened corners.

- be aware of the official requirements for custom declarations, and the local regulations for the export of plants, if they are to be sent directly back home. See 'Customs' below. Dried plants can be regarded for customs purposes as technically dead.
- have enough money to pay for the crates and the postage.
- agree with the local herbarium whether you will return duplicate specimens from home following identification, or whether you will send the specimens straight to the herbarium, and send a list later. Send them from home if at all possible, so you can be absolutely sure what is in the packet (see 5.9 below).
- don't expect the crates to get home for several weeks or possibly months.

5.8 Customs It may be necessary to get written permission to export specimens from the host country. This can sometimes be counter-productive, and local advice should be sought. If you have made contact with a local herbarium, this will solve many of the problems, as they may be able to help with the transport back home, and will be aware of how to deal with customs, postal services, etc. - but don't expect this sort of help to be available unless you have arranged it specifically in advance. For entry into the UK, herbaria here have special Customs 'Privilege Labels' to avoid import problems. These are especially useful if specimens are to be posted. Customs are increasingly opening such packages if not so labelled and can damage specimens. Discuss this with your local herbarium. See note in para. 2.1 about dealing with officialdom.

5.9 When you get home Once you get them home, you will need to transfer them to permanent packets, either as you identify them, or perhaps as a one-off exercise when you get back to check that they have all arrived safely. The danger is that packets and collection data become separated, which is particularly likely if collections remain unsorted. It is important to sort, re-packet, fully label (typed labels and photocopied duplicates) and split into sets for

different herbaria. If a specimen is correctly labelled it does not matter if it remains unidentified for years. Sorting if possible should be done by the specialist who is studying the collection. Separation into duplicates before this has been done is risky, as it may remove evidence of plant associates, and also the ability to search through the material for some taxonomically important component.

5.10 Photography Don't underestimate the value of photography in collecting, both for general habitat views and for individual plant studies. A great deal of skill is necessary for close-up studies of bryophytes, but Edwards (1986) discusses some of the problems of photographing bryophytes in the tropics, and provides useful advice on equipment, magnifications etc. The camera will provide a valuable record, and should be used as a supplement to your other methods of recording information. An Eastman Kodak publication on tropical photography (1986) is included as an appendix in Chapman (1988).

6. Suggested research topics

Although the purpose of this guide is to assist collecting, there may also be opportunity for other types of research.

6.1 Floristics Producing a list of collections is useful in itself, and may merit publication. This will publicise the material for possible use by others, and may add significantly to our knowledge of phytogeography.

6.2 Taxonomic revisions It will quickly become apparent while trying to identify tropical bryophytes how difficult this is, and the great need for regional and world-wide revisions. The latter will often be a very big undertaking, requiring access to a good library, a rich herbarium, and especially access to a loan facility for borrowing material, particularly type specimens. Nevertheless, concentrating your collections on one particular group or genus may provide the foundation for a contribution to such a revision.

6.3 *Ecology* Taxonomic knowledge is a prerequisite for ecological work. There are many possibilities here, and you will either need to have a very good idea in advance about what you are going to do, or have someone on the expedition who is able to give support and advice. You will need to take any equipment you need with you: it is unlikely to be easily available at your destination. Possible areas of investigation are:

- what grows in/at a given area, altitude, habitat, tree, etc.
- what habitats are occupied by a given species or genus
- estimates of bryomass at different sites or altitudes

6.4 *Reproductive biology*

- distribution of sporophytes of a given species in different habitats
- characteristics of sporophyte production between different species in the same habitat
- seasonal distribution of sporophytes (difficult unless you are there long enough)

7. How to distinguish between different bryophytes

Many hints have been provided already on how to distinguish tropical bryophytes sufficiently well to be able to predict the value of collecting them. There are some characteristics of bryophytes that have more importance and significance for identification in the tropics than in temperate regions, and vice versa, but a separate paper is planned on this, and so it is not dealt with here. Although you should use the sources mentioned in the 'Literature on identification' section below as a source of information before you go, only collecting in the field, and work at the end of the day on identifying your collections, will give you a feel for this.

8. Literature on identification

You may not find it easy to find books ('floras') to help with the identification of your bryophyte collection. There are not even lists of known bryophytes for many tropical countries. This position is slowly changing, despite the present lack of knowledge about the tropics. Some areas have been worked much better than others, particularly the richer floras such as those of the Caribbean and South East Asia. Floras covering quite wide areas are now becoming available, for instance Eddy (1988) covers the mosses of the whole of S.E. Asia, and Bartram (1949) is still the most useful book for the mosses of Central America. For the liverworts of tropical America, Gradstein's key for Puerto Rico (Gradstein, 1989) can be used. In other parts of the tropics the position is not as good, but there are projects underway or being considered in most of the tropics, although they may take many years to complete. A very useful general survey of available literature for both individual countries and for genera (Greene and Harrington, 1988, 1989) is now available. These documents should give you pointers to the more general papers on the country in which you are interested. It may still be necessary to chase up references to more detailed, local papers, and the British Museum (Natural History) Botany Library may be able to provide you with photocopies (see below for details). At a higher level, you will find Schofield (1985) very useful for deciding to which group a plant belongs, and there are also generic floras for some parts of the world. Look through the bibliography for these and other books that cover your area. There are much fewer books on liverworts and hornworts than there are for mosses. If there is no local flora in existence, you may be venturing into the area of taxonomic research. It will be then that you benefit from the quality and frequency of your collections, both to get a picture of the variability of the taxa, and also to search for perianths, peristomes, etc., which may be necessary for identification and study.

At a major library such as the British Museum (Natural History), you will find several journals concerned with bryology, such as *Journal of Bryology*, *Lindbergia*, *Journal of the Hattori Botanical Laboratory*, *The Bryologist* and *Cryptogamie*, as well as many journals devoted to particular areas of the tropics. These will often give leads to useful papers about the area you are visiting.

9. Acknowledgements

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10. Bibliography

The following bibliography contains references to publications some of which you may find difficult to locate. The British Museum (Natural History) may be able to provide (quite expensive) photocopies of some of the scientific articles (contact the Library on 01-938 9123), but copies of most items are held by (or have been seen by) the author of this guide, who will be willing to help where possible.

Where prices are quoted, these are as at June 1988 or later.

Abeywickrama, B.A. (1960). The genera of mosses of Ceylon. *Ceylon J. Sci. (Bio. Sci.)* **3(1)**:42-122. [Like other generic keys (e.g. Griffin and Morales (1983), Van der Wijk (1958), Van der Wijk and Chopra (1966)), this is not easy to use, as it requires knowledge of 'phylogenetic' characters that are often difficult to observe.]

Ando, H and A. Matsuo. (1984). Applied Bryology. *Advances in Bryology*: **2**. J. Cramer. [Covers all known uses and potential uses of bryophytes, including medical, ecological (both

as erosion controllers and bioindicators) and biochemical.]

Bartram, E.B. (1939). Mosses of the Philippines. *Philipp. J. Sci.* **68**. Reprint Hbk:DM135. [A useful book for Malaysia as well as the Philippines. The recent reprint is unfortunately very expensive.]

Bartram, E.B. (1949). Mosses of Guatemala. *Fieldiana: Botany* **25**. Chicago Natural History Museum. [A useful book for all parts of tropical America, well-written and easy to use, with good keys, descriptions and illustrations. Still available quite cheaply via the Missouri Botanical Garden, although the nomenclature is somewhat outdated.]

Blashford-Snell, J. and Ballantyne, A. (1977). Expeditions, the Experts' Way. London. [A standard 'how to do it' book.]

Breen R.S. (1963). Mosses of Florida. University of Florida Press, Gainesville. [Florida has a relatively small number of tropical mosses, but this book has good short descriptions and quite good illustrations of most of the common mosses of the Caribbean region.]

Brotherus, V. (1924). Musci (Laubmoose). In: Die natürlichen Pflanzenfamilien, Bd. 10, 11. Engelmann, Leipzig. Reprint, 1978: DM394. [A world-wide summary of all moss families and genera, with brief keys to species.]

Chapman, R. (1988). Tropical Forest Expedition Manual. (3rd ed.). Expedition Advisory Centre (1 Kensington Gore, London SW7 2AR). Pbk. £5. [The EAC is jointly administered by the Royal Geographical Society and the Young Explorer's Trust, and provide an information and training service. This manual is designed for those with limited expedition experience, who are intending to visit a relatively unexplored tropical rain forest area. It covers dress and equipment, movement and navigation, camping and cooking, local assistance, air supply, and some guidance on research topics, as well as appendices on photography and reference sources.]

Croat, T.B. (1979). Use of a portable propane gas oven for field drying plants. *Taxon* **28**: 573-580. [Of more use to those with well-financed logistics.]

Crum, H.A. and Steere, W.C. (1957). Mosses of Puerto Rico and the Virgin Islands. *N.Y. Academy of Sciences* **7(4)**. [Useful for the Caribbean.]

Caulfield, C. (1985). In the Rainforest. Heinemann, London (Hbk:£10.95) and Pan (Pbk:£3.95). [A journalist's account of the nature and fate of tropical rainforest, with emphasis on man's assault on the forest; very well written, most informative, and hard-hitting. Like Myers, this provides plenty of evidence to justify a scientific expedition to the tropics.]

Davies, S.B. et al. (1986). Plants in danger : what do we know. IUCN (International Union for the Conservation of Nature and Natural Resources), Gland, Switzerland and Cambridge, U.K. Pbk:£15. [This is a mine of information on the flora and vegetation of each country in the world, as a background to conservation requirement, although bryophytes don't get a mention. It will provide a useful starting point for selecting a country and finding pointers to further information.]

Delgadillo M., C. (1987). Additional recommendations for bryologists visiting the tropics. *Taxon* **36**: 289-291. [Particularly aimed at professional botanists, and their relations with tropical colleagues during visits, but of relevance to anyone who wants to collect. An addendum to Mori and Holm-Nielson (1981).]

Eastman Kodak. (1986). Tropical Photography. Kodak Publication C-24. [Seven pages of advice on care of equipment and materials, exposures, processing and dealing with fungus. This item is also included as an Appendix to Chapman (1988).]

Eddy, A. (1988). A Handbook of Malesian Mosses Volume 1: Sphagnales to Dicranales. British Museum (Natural History). Pbk:£15. [The first of five parts. Indispensable, containing

keys, descriptions, illustrations and habitat and distribution data.]

Edwards, S.R. (1986). Bryophyte collecting and plant photography. *University of Hull Department of Geography Miscellaneous Series* **30**: 65-72; 102-108. 2 fig. [Describes collecting and photography in Cameroun.]

Fleischer, M. (1902-1922). Die Musci der Flora von Buitenzorg. 4 vols. E.J. Brill, Leiden. (Reprinted in two volumes, 1976. Hbk:DM400). [This is strictly speaking a moss flora of Java, but it covers a large part of the Eastern tropics and is (according to P.W. Richards) „by far the best tropical moss flora ever written, though now of course somewhat out of date“.]

Florschütz, P.A. (1964). Musci of Suriname, Part 1. (Flora of Suriname, Vol. 6 Part 1). E.J. Brill, Leiden. Pbk:DM48. [This is one of the best tropical moss floras, and includes most of the acrocarpous mosses likely to be met with in the lowlands of the Guianas and Amazonia.]

Florschütz-De Waard, J. (1986). Musci, Part 2. (Flora of Suriname, Vol. 6 Part 1.) Pbk:DM38. [Continuation of Florschütz (1964). Includes three families of pleurocarps, including Hookeriaceae.]

Frahm, J.-P. and Gradstein, S.R. (1986). An apparatus for drying bryophytes in the field. *Bryological Times* **38**: 5. [Describes a homemade, portable aluminium frame with a wire mesh shelf, weighing 2.5 kg in total, heated with a kerosene stove, used in Borneo and South America.]

Gifford, N. (1983). Expeditions and Exploration. Macmillan, London. [A book with lots of lists (e.g. what to take, what to put in your medical kit etc.), and advice from those who have planned expeditions or gone on them. An extensive bibliography.]

Gradstein, S.R. (1989). A key to the Hepaticae and Anthocerotae of Puerto Rico and the Virgin Islands. *The Bryologist* **92(3)**: 329-348. [A key emphasising vegetative characters for 237

species in 92 genera of liverworts and hornworts recorded from Puerto Rico and the Virgin Islands; also useful for other parts of tropical America.]

Greene, S.W. (1986). Keeping them dry. *Bryological Times* **38**:6. [Describes how to keep dried specimens dry by adding silica gel to the polythene bags of dried specimens, on a trip to Chilean rain forests.]

Greene, S.W. and Harrington A.J. (1988). The Conspectus of Bryological Taxonomic Literature - 1: Index to monographs and regional reviews. (*Bryophytorum Bibliotheca* **35**). J. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin and Stuttgart. Pbk:DM120 [A worldwide list of taxonomic literature, presented alphabetically by genus and family.]

Greene, S.W. and Harrington A.J. (1989). The Conspectus of Bryological Taxonomic Literature - 2: Guide to national and regional literature. (*Bryophytorum Bibliotheca* **37**). J. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin and Stuttgart. Pbk:DM120 [The indispensable source for the main bryological literature of countries, regions and islands of the world.]

Griffin, D. and Morales, M.I. (1983). Keys to the genera of mosses from Costa Rica. *Brenesia* **21**: 299-323. [Useful key to genera of Central America - over 200 genera are dealt with.]

Fosberg, F.R. and Sachet, M.-H. (1965). Manual for tropical herbaria. (*Regnum Vegetabile* **39**). International Association of Plant Taxonomy, Utrecht. [A very detailed account of herbarium management in the tropics. Covers collecting and labelling as well as herbarium techniques, procedures and administration.]

Hatt, J. (1985). The Tropical Traveller. Pan, London. Pbk:£3.95. [Preparation, equipment, money problems, health, exploring, etc. A very cheap way to get a feel for the problems.]

Herzog, T. (1926). Geographie der Moose. G. Fischer, Jena. Reprinted 1975, DM120. [This is out of date, but is still a good introduction to floristics, including the tropics, for anyone who can read German.]

Jacobs, M. (1988). The Tropical Rain Forest. Springer-Verlag. Pbk:£20.65. [Original Dutch edition published 1981. A well presented and useful general book on the structure, ecology, physiology etc. of lowland tropical rain forests with an emphasis on S.E. Asia. This sort of book is essential as a source book for planning an educational expedition to such areas. It specifically excludes other tropical areas, including upland forests, where bryophytes are likely to be in greater abundance and variety.]

Long, D.G. (1982). Collection and preservation of bryophytes in Arabia. *Bull. Emirates N. H. Gp (Abu Dhabi)* **18**: 18-19. [A brief guide to recognising bryophytes, collecting, packeting, drying and labelling.]

Longman, K.A. and Jenik, J. (1987). Tropical forest and its environment. 2nd ed. Longman, England. Hbk:£17.50 [Excellent account of rainforest ecology in a small comprehensive format; some emphasis on Africa.]

Mitchell, A.W. (1986). The Enchanted Canopy. Fontana/Collins. Pbk:£9.95. [Subtitled 'secrets from the rainforest roof'. Mainly describes animal life, and bryophytes don't get a mention, but lots of beautiful photographs.]

Mori, S.A. and Holm-Nielson, L.B. (1981). Recommendations for botanists visiting neotropical countries. *Taxon* **30**: 87-89. [Aimed at professional botanists, with the items of more general interest already mentioned in this guide. See also Delgadillo (1987) for elaboration of the more specifically bryological points.]

Myers, N. (1984). The Primary Source: Tropical Forests and our Future. Norton and Co. [An important and influential book about the importance of tropical forests to the world. The book contains all the information and arguments you will need to justify a trip to the tropics.]

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- Perry, D. (1986).** Life Above the Jungle Floor. Simon and Schuster. [A popular account of a biologist's discoveries in the tree tops of a Costa Rican jungle, including creating a tree top platform and a network of ropes from which he hung to observe the wildlife.]
- Pócs, T. (1982).** Tropical forest bryophytes. In: A.J.E. Smith (ed.), *Bryophyte Ecology*. Pp. 59-104. Chapman and Hall, London (Hbk:£50). [This is an excellent account of tropical bryophyte ecology, that fills out the more general picture provided by Jacobs (1981) and Whitmore (1984). It gives some idea of what species can be expected in different habitats in different parts of the tropics. Along with Richards (1984), essential.]
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- Richards, P.W. (1984).** The ecology of tropical forest bryophytes. In: R.M. Schuster (ed.), *New Manual of Bryology Vol. 2*, pp. 1233-1270. Nichinan. [Complements Pócs (1982), based on wider geographical area, and with a more detailed review of epiphylls.]
- Schofield, W.B. (1985).** Collecting bryophytes and processing for study. Appendix A (pp 387-391) of *Introduction to Bryology*. Macmillan. Hbk:£35. [A useful general summary of where and when to collect, collecting tools and methods, observations on fresh material, labelling, packeting, filing and storage. The book itself is excellent, and particularly useful for the circumscriptions of each family, which may help in preliminary identifications.]
- Smith, A.J.E. (1978).** The Moss Flora of Britain and Ireland. Cambridge University Press. Pbk:£22.50. [The standard UK text on identifying mosses, covering the whole flora. See also Watson (1981).]
- Steere, W.C. (1944).** Instructions to naturalists in the Armed Forces for botanical field work: No. 3 The collecting of mosses and liverworts. *Supplement to Company D Newsletter*. 1-13. Company D, 3651 S.U. Department of Botany, University of Michigan, Ann Arbor, USA. [Covers how to collect, where to look, how to document etc. A previous (and quite successful) attempt to cover a similar area to that of this guide, but now out of date in its approach to collecting.]
- ter Steege, H. and Cornelissen, J.H.C. (1988).** Collecting and studying bryophytes in the canopy of standing rain forest trees. In J.M. Glime (ed.) *Methods in Bryology*, pp. 285-290. Hattori Botanical Laboratory, Nichinan. [Briefly reviews possible methods of tree climbing and gives details of the method the authors used in French Guiana - using various rope climbing techniques, which are described. Several bryophyte species new to Guyana were found in the canopy.]
- Van der Wijk, R. (1958).** Precursory studies on Malaysian Mosses II. A preliminary key to the moss genera. *Blumea* **9**: 142-186. [Usefully generally for tropical Asia.]
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Walter, H. (1971). Ecology of tropical and subtropical vegetation. Ed. J. Burnett, Oliver and Boyd, Edinburgh. [This book deals with high mountains, savannas, deserts, etc., which are not dealt with in Jacobs, Richards and Whitmore.]

Watson, E.V. (1981). British Mosses and Liverworts. Cambridge University Press. Pbk:£27.50. [A less comprehensive text than Smith (1978) for mosses (only abbreviated descriptions of the uncommon species), but includes liverworts (unlike Smith). Essential for the beginner who is serious about getting to know British bryophytes.]

Whitmore, T.C. (1984). Tropical Rain Forests of the Far East. (2nd ed.) Clarendon Press, Oxford. Pbk:£25; hbk:£50. [Of general, world-wide interest, despite the title. Rather more academic than Jacobs (1981), and more up to date on literature than Richards (1952).]

Whittier, H.O. (1976). Mosses of the Society Islands. University of Florida Presses, Gainesville. [Good for Pacific Island genera, even if the species are different.]

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Research needs and priorities

(1-4 modified from Gradstein (1995))

- (1) Taxonomic revisions in important genera to allow identification of specimens of difficult groups.
- (2) As complete as possible inventories of different forest stands of different forest types.
- (3) Comparisons of disturbed and undisturbed forests to assess the human impact.
- (4) Studies on the ecology and reproductive biology of common and rare species.
- (5) Preparation of checklists for countries or provinces as a base of all bryological studies.
- (6) Preparation of registers of collections.
- (7) Mapping of the registered data to obtain first ideas about the vertical and horizontal distribution.
- (8) Mapping of the diversity of bryophyte species per square unit (1 ha, 10 x 10 km, a province) in different parts of a country to get an estimate of the location of hot spots and species rich areas, which can be proposed for conservation.
- (9) Preparation of red lists of endangered species for countries and provinces to be submitted to conservation authorities.
- (10) Start of bioindication studies in urban areas or human influenced regions.

Gradstein, S.R. 1995. Biodiversity of non-vascular epiphytes in tropical rain forests. FIBAL Scientific report, Second international ESF-workshop on tropical canopy research, Schloß Reisenburg, 27.-30. July 1995.

INSTRUCTIONS TO AUTHORS

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