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Scientific Results of the BRYOTROP Expedition to Zaire and Rwanda
2. The altitudinal zonation of the bryophytes on Mt. Kahuzi, Zaire

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Abstract. The altitudinal zonation of the tropical rain forest at Mt. Kahuzi has been studied using bryophytes. The study is based on floristic parameters such as the number of species per hectarplot in different altitudes and the calculation of floristic discontinuities extracted from an evaluation of altitudinal ranges. The results are compared and correlated to ecological parameters, especially data on the phytomass of epiphytic bryophytes per m^2 and per hectare. Based on these data, the tropical rain forest is classified as submontane forest (- 1500 m), lower tropical montane forest (1500 - 2000 m), upper tropical montane forest (2100 - 2800 m), and subalpine forest (2900 - 3200 m). Except for the terminology, the vegetation belts derived from bryophytes can be correlated with those presented in general vegetational schemes for tropical Africa.

The phytogeographical situation of Africa is much different when compared to other parts of the tropics. This primarily concerns the low number of species, especially trees: Africa has only one third of the estimated number of flowering plants of the Neotropics and distinctly fewer than SE-Asia (Gentry 1982). In Ivory Coast, only a quarter of the tree species per unit is found than in Malaysia, even though Ivory Coast is reletively rich in species compared to other regions of Africa and even has a higher ecological diversity than SE-Asia (Hamilton 1982). Forests are dominated by a few or even a single species which is the reason why only the African forests have been partly phytosociologically classified. Especially the high altitude forests are very homogenous when compared to, for instance, the Andes. The paucity of species is also reflected in the number of pteridophytes (Tryon 1989). There are 120 genera with 2100 species of pteridophytes in tropical America, but only 80 genera with

500 species (23.8%) in tropical Africa, and 190 genera with 3200 species in Malesia.
Also the altitudinal zonation differs from other parts of the tropics. A major difference is the presence of a bamboo belt between 2300 and 3000 m. Proposals of the altitudinal zonation of forests and vegetation belts usually classify the lower 2000 meters (which is about half of the vertical distance) as "lowland forest belt" (Hamilton 1982, Hedberg 1951). This is probably not because there is no zonation below 2000 m but because these models have been developed in East Africa, where regions below 2000 m are lacking.
Therefore it is a great advantage that in the BRYOTROP-project (Frahm 1993) the transect investigated (for a description see Fischer 1993) covered an altitudinal range from 900 to 3300 m at Mt. Kahuzi and to 4500 m at Mt. Karisimbi.
As pointed out by Frahm & Gradstein (1991), bryophytes are an excellent tool for the study of the altitudinal zonation of tropical rain forests. The botanical parameters usually used are the physiognomy of forests, height, leaf sizes or quantity of lianas and epiphytes. In contrast, bryophytes are climatic indicators for temperature and humidity, have much more wider ranges and are fewer in species.
The altitudinal zonation of tropical rain forest based on bryophytes can be classified by ecological or floristic parameters. Ecological parameters such as percentage cover of bryophytes on bark of trees or on rocks and soil have been used in Colombia by van Reenen & Gradstein (1984). Phytomass of epiphytic bryophytes per square meter or per hectare or the water storing capacity have been used in Peru (Frahm 1987) and Borneo (Frahm 1990a). Also in Borneo, the ordination of epiphytic bryophytes (Kürschner 1990) as well as life forms and morphological structures (Frey et al. 1990) were utilized along an altitudinal transect.
Altitudinal zonation based upon the vertical distribution of species has been studied in Peru (Gradstein & Frahm 1987), New Guinea (Enroth 1990)and at Mt. Kilimanjaro (Pócs 1991). A floristic zonation can be obtained by comparing the total number of species per square unit or by analysing the lowermost and uppermost occurrences of species (floristic discontinuities).
The results of studies on the altitudinal zonation of tropical rain forest in Colombia, Peru, New Guinea and Borneo using bryophytes have been summarized by Frahm & Gradstein (1991) and have been used to propose a general scheme of altitudinal zonation for tropical rain forests.

Except for a small study on the altitudinal zonation of Mt. Kilimanjaro (Pócs 1991), there are so far not any studies available on the altitudinal zonation of tropical rain forests in Africa based on bryophytes. During the BRYOTROP expedition to Zaire and Rwanda, floristic and ecological data were collected along the transect studied. The transect is described by Fischer (1993).

1. Floristic Zonation

The floristic zonation is based on approximately 2500 samples of bryophytes collected along the BRYOTROP transect in Zaire (Mt. Kahuzi 850 - 3300 m) and Rwanda (Nyungwe forest 1500 - 2500 m, Mt. Karisimbi 2700 - 4500 m). Data were processed with the database program dBase III + ., facilitating evaluation of the data required for the altitudinal zonation.

1.1 Number of species per relevée.

For every relevée studied in 200 m altitudinal distance, the total number of species was determined, giving an indication of the increase in species the higher the altitude. The increase in species with altitude is very much characteristic of bryophytes in the tropics but not for other groups of organisms, where the total species diversity decreases with increasing altitude and latitude. Generally, many groups of animals as well as flowering plants show their highest species diversity in the tropical lowlands. This may, however, not be generalized. Also pteridophytes seem to show a similar increase in species numbers with the altitude as in bryophytes (Tryon 1989), which is not surprising. Pteridophytes, although commonly regarded as cormophytes, have a "weak point" in

their life cycle which is the gametophyte. The gametophyte, however, is morphologically and physiologically nothing other than a thallose liverwort gametophyte, which drastically reduces the occurrence of ferns.
The size of a relevée is about a hectare and therefore the number of bryophyte species give an idea of the species richness per square unit (fig. 1) and allow comparisons with data from other parts of the world.
In the lowermost part of the transect at Irangi, Zaire, a comparatively low species number of 31 was found in 900 m altitude. Even along a river at 850 m in a humid riverine forest with collections from the river bed, the number did not exceed 39. The number of species remained at 30 at 1100 m and increased only slightly at 1300 m and 1500 m to 40 viz. 38 species.
The collections from the Nyungwe Forest in Rwanda between 2000 and 2400 m altitude included Lobelia bogs with Erica heath (with up to 81 species), a swamp forest with 51 species and wet, rocky slopes with 50 species, all not belonging to the zonal vegetation. Confined to zonal forest relevées, there were 44 species collected at 2000 m altitude at the bottom of a valley, but even fewer species in elevations up to 2400 m on a relatively dry slope. Sixty-three species were collected in a *Hagenia-Podocarpus*-forest in 2400 m.
At Mt. Biega in Zaire, species numbers per relevée varied much due to different vegetation types. There were only 20 species in bamboo forests or 22 in *Hagenia* forests at 2500 m but considerably more species in mixed forest (28 at 2100 m, 36 at 2300 m, 55 at 2400 m). Highest values were reached in the *Erica* vegetation at the top of Mt. Biega at 2600 m with 71 species.
At Mt. Kahuzi, the number of species per relevée varied again due to different vegetation types. A high number of 62 species was found in a forest at 2000 m. Although pure bamboo stands are not taken into consideration here, the number of bryophyte species in the small forest patches within the bamboo belt did not exceed 44 at 2300 m viz. 45 at 2600 m altitude, thus being lower than at 2000 m. Also relevées in rock or shrubby areas on a ridge at Mt. Kahuzi cannot taken into account. The highest value was found in the *Podocarpus* forest and *Erica* heath at 3200 m with 75 species.
Due to the Massenerhebungseffekt, the highest values on Mt. Karisimbi are at higher altitudes with a maximum of 91 species at 3700 m. There were 34 species in *Hagenia* forests at 3000 m but 77 species in *Hypericum-Senecio* vegetation at 3400 m. Above 3700 m, the species numbers declined to 29 in subalpine *Senecio-Lobelia* vegetation at 3900 m, 20 in alpine *Alchemilla* vegetation at 4200 m and only 9 species at the rocky summit.
The curves of species numbers for the different parts of the transect are shown in fig. 1.
Due to the different location of the parts of the transect, the different climate and geology, and the different elevation of the mountains studied, the various parts of the transect are not comparable and therefore the species curves in fig. 1 are separate for every part of the transect. However, for an attempt all values have been integrated into one curve (fig. 2), with the exception of the values for Nyungwe Forest and Mt. Biega. These are all elevations which are covered in other parts of the transect but not as representative. Nyungwe Forest is omitted here because it is drier and the altitudinal zonation is partly reversed due to depressions filled with cold air; Mt. Biega because it is close to Mt. Kahuzi but lower and therefore with a generally lowered zonation.
The curve (fig. 2) shows three segments: a lower part with fewer than 40 species in elevations up to 1500 m, 40 - 70 species in elevations between 2000 and 2600 m (a relevée between 1500 and 2000 m at 1700 m was not studied) and highest values with 70-90 species above 2600 m. The lower part (< 40 species) can be attributed to the lower montane forest, the middle part (40-70 species) to the upper montane forest and the upper part (> 70 species) to the subalpine forest.
In an analysis of the altitudinal distribution of Kilimanjaro bryophytes, Pócs (1991) found an increase of species numbers in 100 m intervalls to 1800 m and two peaks at 2500 and 2900 m as well as a decrease above the forest line between 3000 - 4000 m elevation and an absolute minimum above the subalpine heath vegetation.

Generally there is an increase in the number of

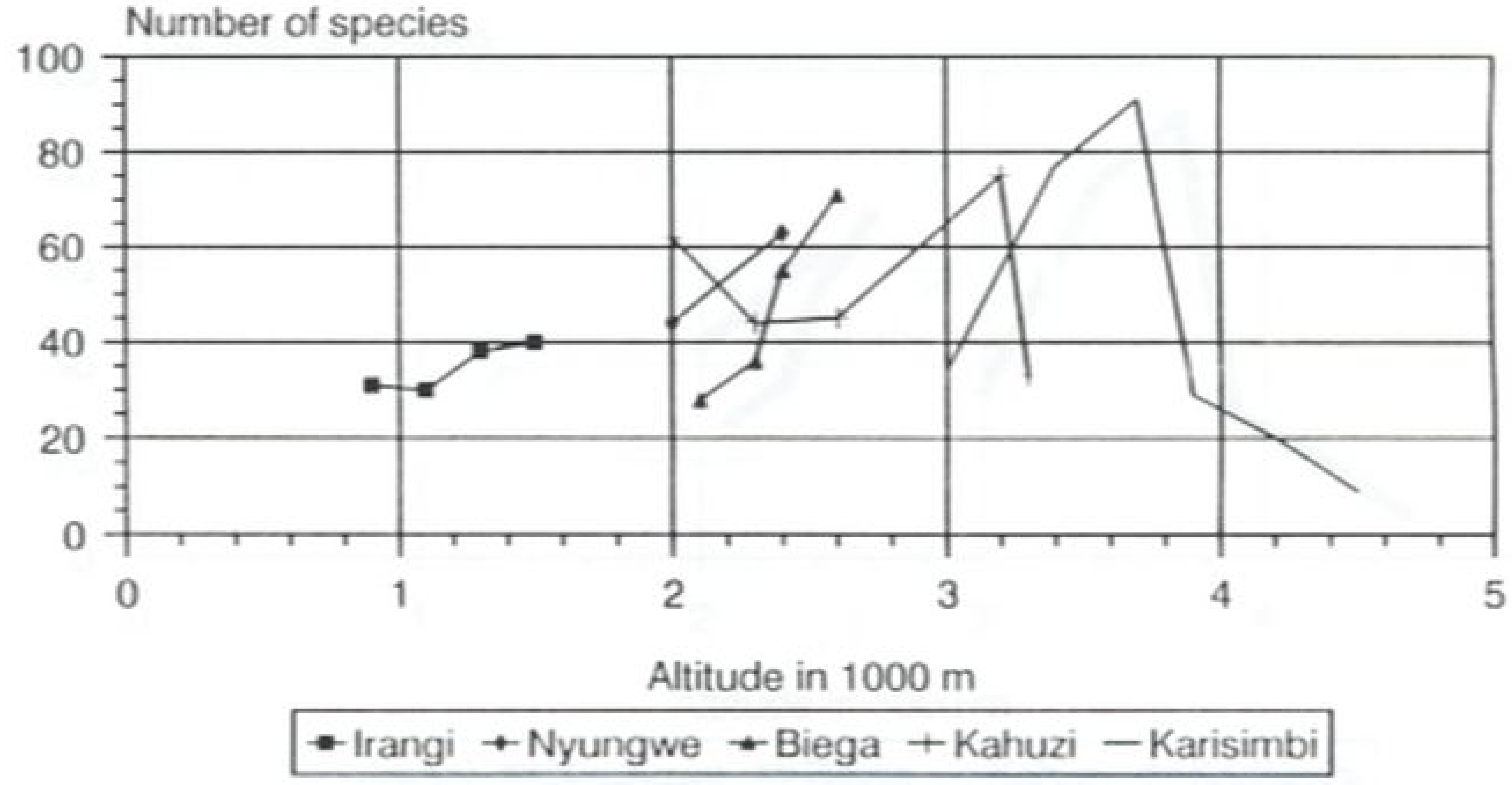

Fig. 1. Number of bryophyte species per relevée (c. one hectare) along the BRYOTROP transect in Zaire and Rwanda.

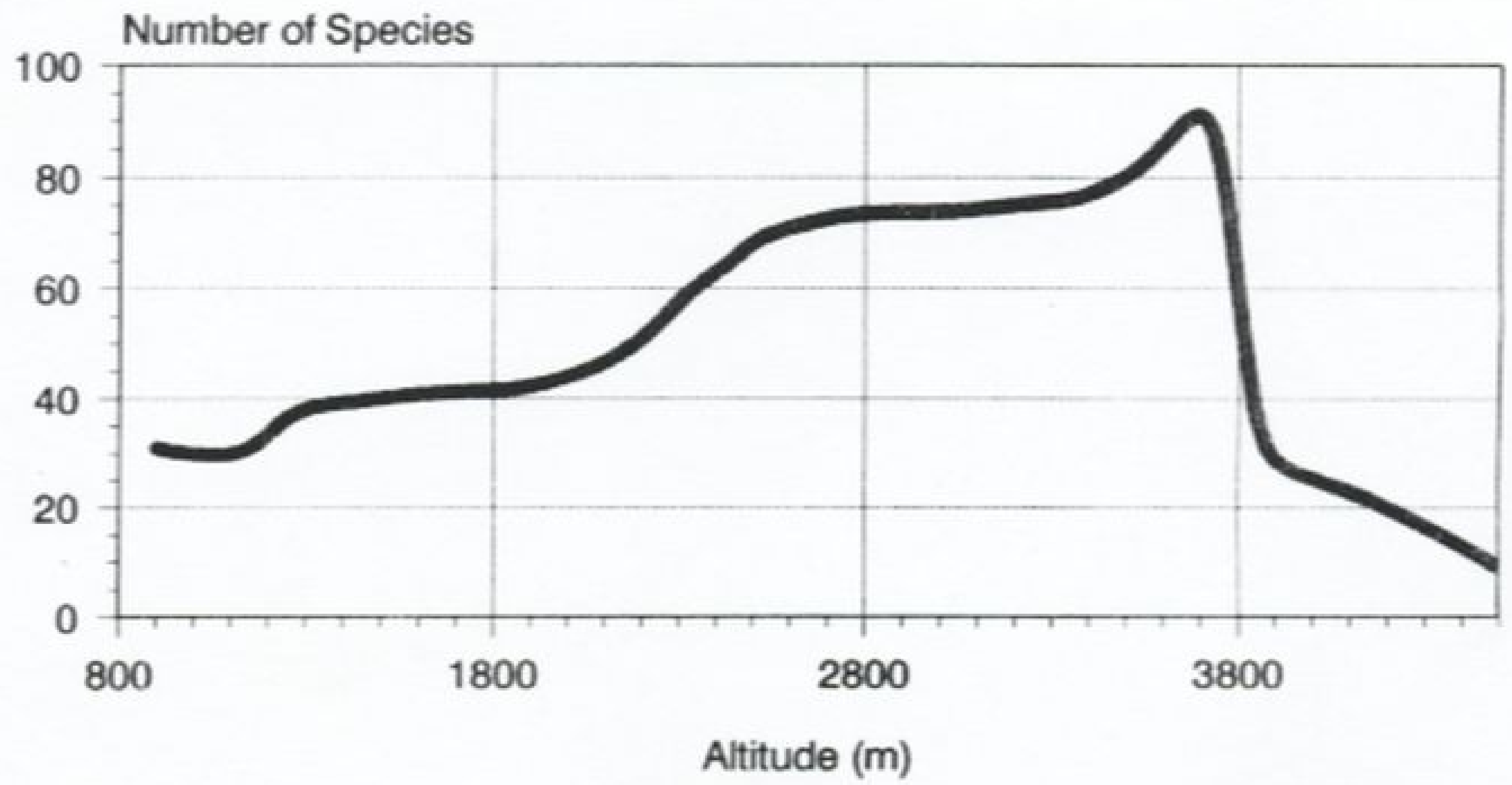

Fig. 2. Number of bryophyte species per relevée (c. one hectare) along the BRYOTROP transect in Zaire and Rwanda. The species numbers from the different parts of the transect are integrated.

species from the lowlands to the forest line (and a sudden decrease above the forest line). This is in accordance with the increase of the phytomass and cover of bryophytes with elevation and probably a worldwide effect. It reflects the increase in precipitation and humidity and the decrease in evaporation and temperatures as well as the fact that the majority of tropical bryophytes are cold adapted species with their main occurrence in the tropical mountains with only few species being adapted to the tropical lowland climate.

1.2 Comparison with the extra-tropics

The values of species numbers per relevée in different altitudes in Zaire and Rwanda obtained during the Bryotrop-expedition allow an interesting comparison with extratropical forests, providing an answer to the question whether the tropics are richer in species per square unit or not.

Since data of species numbers from hectarplots in temperate forests appear to be lacking, a similar survey of the bryophyte species was made in the Vosges Mountains, France. In 1992/93, forests with a natural composition and used only by selective wood cutting were chosen in different altitudes and all bryophyte species were listed. Such forests can be regarded as representative for the temperate forests in Central Europe. Between 400 and 900 m (=temperate montane forest), species numbers of 40-60 were found. These are values which were found in Central Africa in the upper montane forest between 2000 and 2600 m. In contrast to the tropics, however, the number of epiphytes is much lower (20-25%, although very high for Central Europe), and the percentage of epipetric species is much higher (about 50%).

1.3 Liverwort-Moss index

The ratio between the number of species of hepatics and mosses is usually used to characterize the oceanity of a climate, based on the observation that hepatics are more numerous in oceanic regions and less common in continental ones. In the tropics, the liverwort - moss index can be used to compare the humidity of different regions or habitats. For the Kahuzi transect in Zaire, the total number of hepatics and mosses per elevation was determined (fig. 3) and the index between mosses and hepatics calculated (fig. 4). Surprisingly, there is nearly no difference between the number of hepatics and mosses along the transect except for the relevée at 3200 m, which was an exceptionally humid Podocarpus stand. Accordingly, the index between mosses and hepatics is roughly 1 along the whole transect except for the relevée in 3200 m, where nearly twice as many species of hepatics were found than mosses. The low index in all altitudes except for 3200 m may reflect the presumably low precipitation in the Kahuzi National Park (metereological data are not available) and relatively dry rain forest types as compared with the other BRYOTROP transects in Peru and Borneo.

Along a transect in Colombia, van Reenen & Gradstein (1984) estimated the percentage cover of hepatics and mosses on tree trunks as well as on soil and rock. Above 1500 m, the authors found almost twice as much hepatics than mosses on soil and rocks and more than five times as many hepatics on tree trunks, indicating a much higher humidity at least at higher elevations. In New Guinea, the number of hepatics was the about the same as the number of mosses in elevations between 1500 m and 3000 m but less below and above this elevation (Enroth 1990).

2. Floristic discontinuities

The altitude, at which a maximum number of species has its uppermost or lowermost occurrence, is regarded as the altitude with the highest degree of floristic change. This is the basis, on which floristic dicontinuities were determined along the transect in Peru (Gradstein & Frahm 1987). For the transects in Zaire and Rwanda, the necessary data were extracted from the collection database. Since not all taxonomic groups encountered have been identified so far, only identified species could be taken into account. This excludes e.g. Hookeriaceae, Leucobryaceae, Meteoriaceae, and

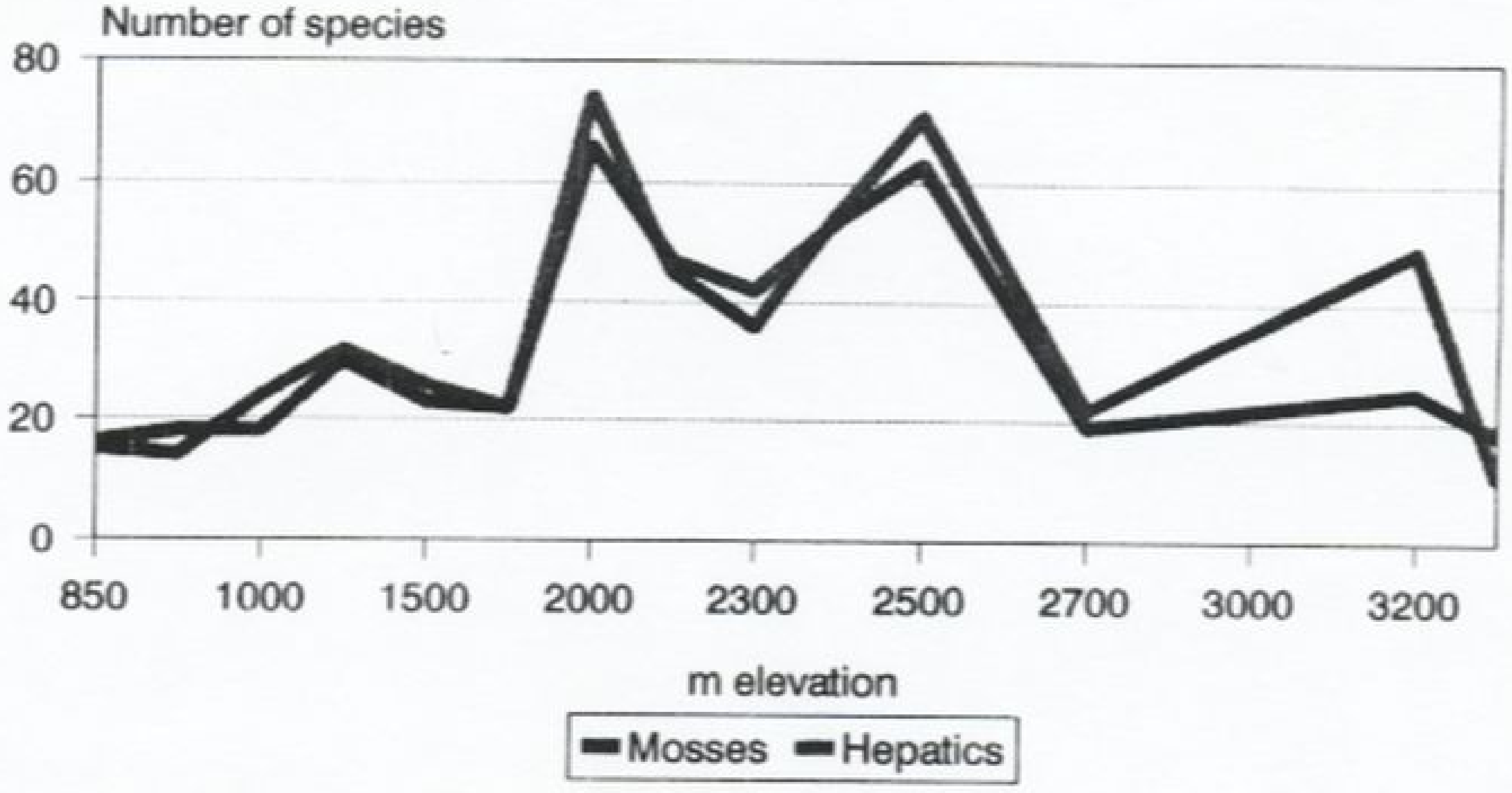

Fig. 3. Number of species of mosses and hepatics along the BRYOTROP transect in Zaire and Rwanda.

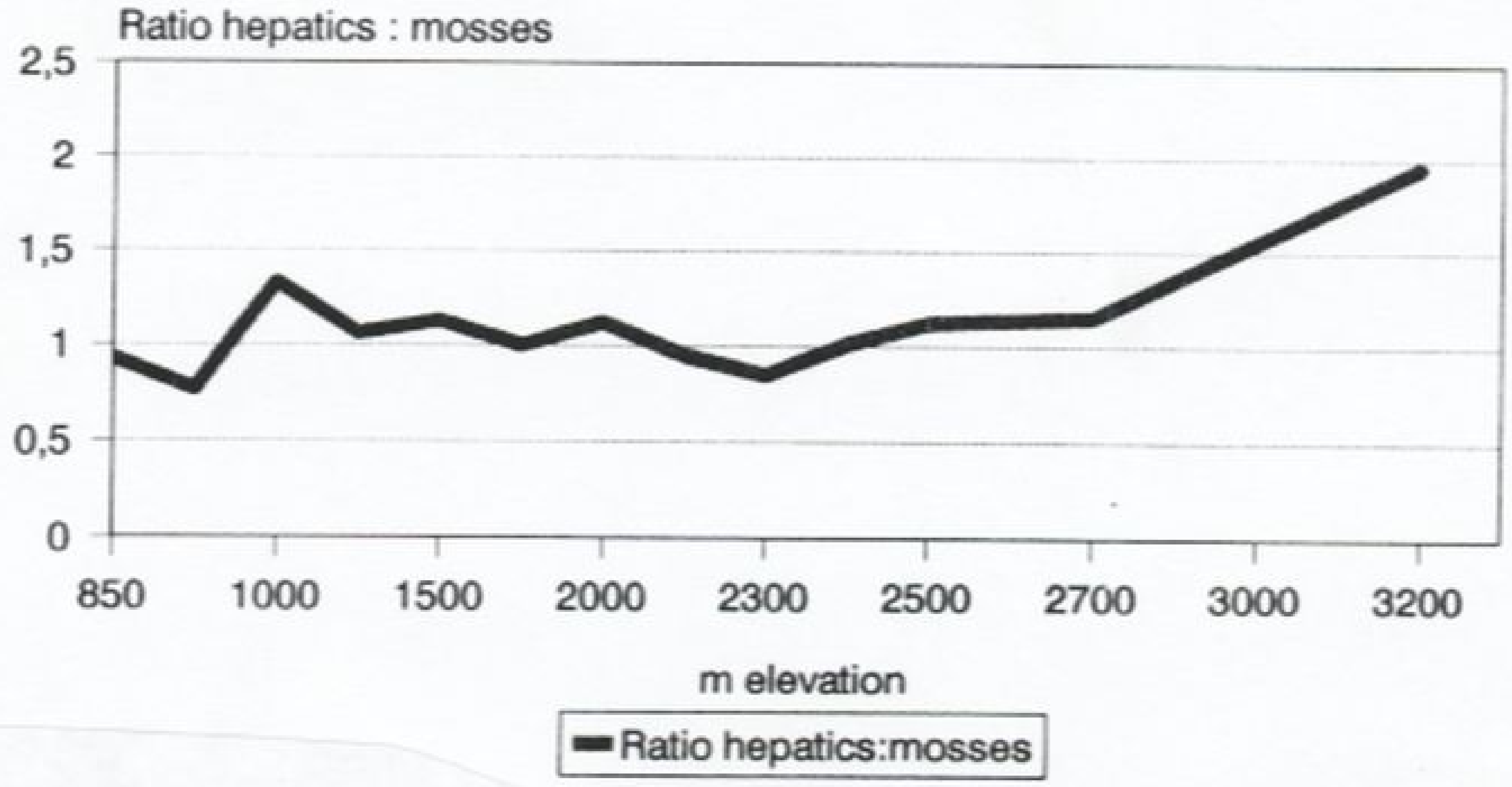

Fig. 4. Moos/hepatic index along the BRYOTROP transect in Zaire and Rwanda.

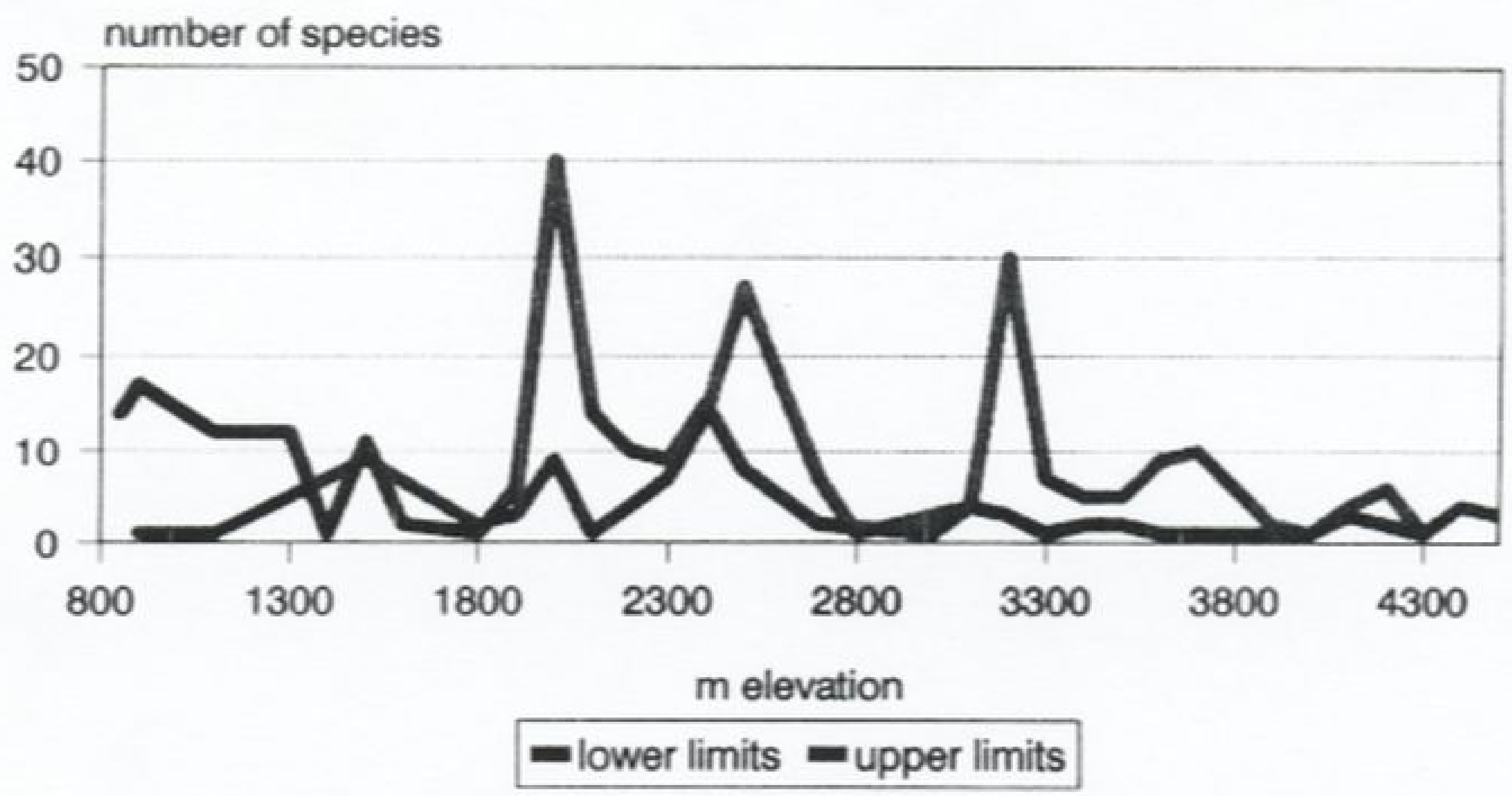

Fig. 5: Floristic discontinuities along the BRYOTROP transect in Zaire and Rwanda.

species-rich genera such as *Lepidozia* and *Bazzania*. Furthermore, only species showing an altitudinal range could be used, thus excluding all single collections or collections from a single altitude. Other limitations of this method are that less frequent species can be lacking in one of the relevées or collected just by chance in others. At least some species are confined to special habitats such as stems of bamboo, peat or rocks, which are not found at all elevations, or are even speific to a perticular altitudinal range. The data also include the de-alpine occurrences of alpine or subalpine species (e.g. *Dicranum johnstonii*, *Chandonanthus hirtellus* or *Campylopus jamesonii*) on open habitats such as rocks, cliffs and roadside cuts at lower elevations. In total, exactly two hundred species of mosses and liverworts were evaluated from all transects. A restriction to species of comparable habitats (e.g. only epiphytes) and comparable relevées would perhaps have been better, but this would have reduced to the total number of species by too much.

Despite of the methodological limitations, the results (fig. 5) are convincing. The curve shows three major peaks at 2000 m, 2500 m and 3200 m elevation. There are 40 of 200 species of bryophytes having their lowermost occurrence at 2000 m, showing a sharp floristic contrast to the elevations below. Another fourteen species start at 2100 m, ten at 2200 m, fifteen at 2400 m. Lower limits are also found between 4000 and 4300 m (lower limits of alpine species) and between 3100 and 3500 m (lower limits of subalpine species), but not inbetween. Small peaks of upper limits are found at 1300 and 1500 m and at 2000 m. A maximum value of 27 species with upper limits are found at 2500 m, and if the elevation between 2300 and 2700 m is taken into account, a total of 72 bryophyte species have their upper limit in this belt. Another distinct mark of floristic change is found at 3200 m, where 30 species were found to have their uppermost occurrence. Sixty-six species ascend up to between 3200 and 3700 m.

If it is taken into account that the collections were not complete at every altitude and that there is also a certain scatter effect, the differences between the maxima and minima are quite impressive. For example, there are 40 species having lowermost occurrences at 2000 m but none at 2800 or 2900 m. Twenty-seven species have their uppermost occurrence at 2500 m but only one at 2800 or 2 at 2900 m. So the curve minima in fig. 3 can be interpreted as elevations with low floristic discontinuities but high floristic homogenity and successfully used for an altitudinal zonation. The effectiveness of this method is furthermore demonstrated by the fact that the floristic changes are not in between the different parts of the transects but within single transects. This is the case with the change at 1500 m within the Irangi-transect, and at 2500 and 3200 m within the Kahuzi-transect.

Species confined to the elevations < 1500 m are:

Acroporium prioninphylax Buck
Barbula eubryum C. Müll.
Barbula indica (Hook.) Spreng.
Calymperes afzelii Sw.
Campylopus decaryi Thér.
Campylopus hensii Ren. & Card.
Ceratolejeunea calabariensis Steph.
Chiloscyphus fragrans (Moris & DeNot.)Engler & Schuster
Ectropothecium perrotii Ren. & Card.
Fissidens leucocinctus Hampe
Fissidens bryum C.Müll.
Fissidens cryptarum C.Müll.
Fissidens cuynetii Biz.
Fissidens glaucissimus Welw. & Duby
Fissidens glauculus C. Müll.
Fissidens microcarpus Mitt.
Fissidens sarcophyllus C.Müll.
Fissidens sciophyllus Mitt.
Homaliodendron piniforme (Brid.)
Hyophila involuta (Hook.) Jaeg.
Lejeunea cataractarum Pócs
Lejeunea confusa E.W.Jones
Leucophanes angustifolium Ren. & Card.
Leucophanes molleri C. Müll.
Lopidium hemiloma (C. Müll.) Fleisch.
Marchantia debilis Goebel
Marchesinia excavata (Mitt.) Steph.
Neckeropsis hookeriacea (C.M ll.) Fleisch.
Neckeropsis lepineana (Mont.) Fleisch.
Octoblepharum sp.
Philonotis mniobryoides Broth.
Plagiochila neckeroidea Mitt.
Plagiochila praemorsa Steph.
Plagiochila salvadorica Steph.
Porella subdentata (Mitten) Jones
Porotrichum elongatum (Wel. & Duby) Gepp.
Prionolejeunea grata (Gott.) Schiffn.
Ptychanthus striatus (Lehm. & Lindenb.) Nees
Pyrrhobryum spiniforme (Hedw.) Mitt.
Radula appressa Mitt.
Radula flaccida Lindenb. & Gott.
Sematophyllum subsimplex (Hedw.) Mitt.
Syrrhopodon armatus Mitt.
Syrrhopodon incompletus Schwaegr.
Taxilejeunea pulchriflora Pearson
Thuidium chenagonii C.Müll. ex Ren. & Card.
Thysananthus spathulistipus (Reinw. et al) Lindenb.
Trichostomum brachydontium Br.
Vesicularia perpallida (C. Müll.) Broth.

Species occurring between 1500 m and 2100 m are:

Acrolejeunea emergens (Mitt.) Steph.
Acroporium pungens (Hedw.) Broth.
Calymperes lonchophyllum Schwaegr.
Campylopus robillardei Besch.
Cephaloziella vaginans Steph.
Clasmatocolea vermicularis (Lehm.) Grolle
Cololejeuna zenheri (Steph.) E.W.Jones
Diplasiolejeunea symoensii Vanden Berghen
Lejeunea tabularis (Spreng.) Spreng.
Lejeunea acuta Mitt.
Lejeunea villaumei (Steph.) Grolle
Lopholejeunea abortiva (Mitt.) Steph.
Notoscyphus lutescens (Lehm. & Lindenb.) Mitt.
Plagiochila intermedia Steph.
Polytrichum subpilosum P.Beauv.
Pseudoleskeopsis claviramea (C. Müll.) Thér.
Radula allamanoi Gola
Schlotheimia brachypoda Thér. et Nav.
Sematophyllum flavovesiculosum Buck
Vesicularia oreodelphus (C. Müll.) Broth.
Vesicularia sigmangia (Broth.) Broth.

Only below 2100 m were found:
Campylopus praetermissus J.-P.Frahm
Erythrodontium squarrosum (Hampe) Par.
Fissidens porrectus Mitt.
Fissidens bryum C. Müll. ex Dus.
Fissidens porrectus Mitt.
Frullania ericoides (Nees) Mont.
Lejeunea caespitosa Ldbg.
Radula boryana (Web.) Nees ex Mont.
Radulina borbonica (Bl.) Buck
Rectolejeunea rhodesiae (Sim) S. Arnell
Syrrhopodon lamprocarpus Mitt.
Syrrhopodon parasiticus (Brid.) Besch.
Taxilejeunea conformis (Mont.) Steph.
Wijkia trichocoleoides (C. Müll.) Crum

Species found between 2100 m and 2800 m are:
Aneura pseudopinguis (Herz.) Pócs
Anthoceros myriandroecium Steph.
Anthoceros sambesianus Steph.
Aphanolejeunea mamillata (Aongstr.) Steph.
Blepharostoma trichophyllum (L.) Dum.
Brachthecium vellereum (Mitt.) Jaeg.
Brachythecium implicatum (Hornsch.) Jaeg.
Brachythecium salebrosum (Web. & Mohr) Schimp.
Brachythecium vellereum (Mitt.) Jaeg.
Breutelia diffracta Mitt.
Bryohumbertia flavicoma (C.Müll.) Frahm
Calymperes erosum C.Müll.
Calyptothecium hoehnelii (C.Müll.) Argent
Campylopus hildebrandtii (C.Mnll.) Jaeg.
Campylopus paludicola Broth.
Cephalozia africana Vana
Cephalozia bicuspidata (L.) Dum.
Cheilolejeunea montagnei (Gott.) Steph.
Chryso-hypnum frondosum (Mitt.) Buck
Clasmatocolea vermicularis (Lehm.) Grolle
Cololejeuna zenheri (Steph.) E.W.Jones
Cylindrocolea atroviridis (Sim) Vana
Dicranella pertenella C.Mnll. ex Dusen
Dicranella subsubulata (C.Mnll.) Jaeg.
Dicranoloma billardieri (Brid.) Par.
Diplasiolejeunea cornuta Steph.
Diplasiolejeunea kraussiana (Lindenb.)Spruce
Dumortiera hirsuta (Sw.) Nees
Entodon adyris Buck
Fissidens bryoides Hedw.
Fissidens androgynum Bruch ex Krauss
Fissidens flavolimbatus Berch.
Fissidens pachylomadelphus Dem. et P. de la V.
Fissidens purpureocaulis C. Müll.
Frullania angulata Mitten
Frullania apicalis Mitt.
Frullania depressa Mitten
Frullania variegata Stephani
Haplomitrium blumei
Hedwigia ciliata (Hedw.) P. Beauv.
Hedwigidium integrifolium (P. Beauv.) Dix.
Hylocomiopsis cylindricarpa
Isopterygium hygrophilum Broth. in Mildbr.
Jamesoniella purpurascens Steph.
Leiomela africana Thér. & Nav.
Lejeunea ramosissima Steph.
Lejeunea capensis Gott.
Lejeunea cyathearum E.W.Jones
Lejeunea eckloniana Ldbg.
Lejeunea helenae Pears.
Lejeunea tabularis (Spreng.) Spreng.
Lejeunea xanthocarpa (Lehm. & Lindenb.) Evans
Leucolejeunea xanthocarpa (Lehm. & Lindenb.)Evans
Marchantia pappeana Lehm. ssp. *pappeana*
Metzgeria nudifrons Steph.
Microcampylopus laevigatus (Thér.)Giese & Frahm
Microlejeunea africana Steph.
Mittenothamnium frondosum (Mitt.) Card.
Mittenothamnium reptans (Hedw.) Card.
Neckera platyantha (C.Müll.) Par.
Neckera remota Bruch & Schimp. ex C. Müll.
Orthotrichum firmum Vent.
Pallavicinia lyellii (Hook.) Carruth.
Phaeoceros carolinianus (Mich.) Prosk.
Phaeoceros fulvisporus (Steph.) Hasegawa
Philonotis hastata (Duby) Wijk & Marg.
Physcomitrium subspathulatum Thér. et Nav.
Plagiochila barteri Mitt. ssp. barteri
Plagiochila heterostipa Steph.
Plagiochila lastii Mitt.
Plagiochila squamulosa Mitt.
Plagiothecium neckeroideum Schimp.
Plagiothecium nitens Dix.
Pylaisiella frahmii Buck
Radula comorensis Steph.
Radula quadrata Gott.
Rectolejeunea brittoniae Evans

Rhabdoweisia fugax (Hedw.) B.S.G.
Rhacopilopsis kilimandscharica (Broth.) Buck
Rhynchostegium brachypterum (Hornsch.) Jaeg.
Rhynchostegium horridum Broth.
Rhynchostegium omocrates Buck
Schiffneriolejeunea altimontana VandenBerghen
Schiffneriolejeunea pappeana (Nees) Gradstein
Schimperella bello-intricata (C.Müll.) Buck
Schimperella katalensis (Leroy) P. Varde
Schoenobryum robustum (Broth.) Frahm
Scopelophila ligulata (Spruce) Spruce
Sematophyllum cellulosum Buck
Sematophyllum nebulosum Buck
Sematophyllum stylites Buck
Symphyogyna brasiliensis Nees & Mont.
Syrrhopodon asper Mitt.
Taxiphyllum laxalare Buck
Tortula fragilis Tayl.

Species found between 2800 m and 3200 m (partially also above) are:

Adelanthus lindenbergianus (Lehm.) Mitten
Anastrophyllum auritum (Lehm.) Steph.
Asterella abyssinica (Gottsche) Grolle
Atractylocarpus alticaulis (Broth.) Williams
Bartramia afro-ithyphylla Broth.
Brachythecium plumosum (Hedw.) Schimp.
Bryoerythrophyllum campylocarpum (C.Müll.) Crum
Campylopus flaccidus Ren. & Card.
Campylopus dicranoides Thér. & Nav.
Campylopus johannis-meyeri (C.Müll.) Kindb.
Campylopus nivalis (Brid.) Brid.
Campylopus schmidii (C.Müll.) Jaeg.
Ceratodon purpureus (Hedw.) Brid.
Herbertus subdentatus
Herzogiella cylindrocarpa (Card.) Iwats.
Hypnum cupressiforme Hedw. var. *mossmanianum*
Hypnum cupressiforme Hedw. var. *lacunosum* Brid.
Hypnum cupressiforme var. *townsendii* Ando
Lejeunea hepaticola Steph.
Leptodontium flexifolium (With.) Hampe ex Lindb.
Leptoscyphus fuscatus Mitt.
Paraleucobryum longifolium (Hedw.) Loeske
Plagiochila barteri Mitt. ssp. *colorans* Pócs.
Plagiomnium rhynchophorum (Hook.) T.Kop.
Plagiothecium nitidifolium (Mitt.) Jaeg.
Pogonatum urnigerum (Hedw.) P. Beauv.
Porotrichum variifolioides De Sloover
Rhabdoweisia africana Dix. & Nav.
Rhacocarpus purpurascens (Brid.) Par.
Sematophyllum brachytheciiforme (Broth.) Broth.
Syzygiella concreta (Gott.) Spruce
Syzygiella geminifolia (Mitt.) Steph.
Tetralophozia cavallii
Tritomaria exsecta (Schmid.) Loeske
Warnsdorfia fluitans (Hedw.) Loeske

The following species range from 2100 m to 3200 m (some also higher):

Adelanthus decipiens (Hook.) Mitt.
Andrewsianthus bilobus (Mitt.) Grolle
Aphanolejeunea exigua Evans
Breutelia stuhlmannii Broth.
Calypogeia afrocoerulea E.W. Jones
Campylopus flexuosus (Hedw.) Brid.
Campylopus jamesonii (Hook.) Mitt.
Chandonanthus hirtellus
Cheilolejeunea cf. pluriplicata (Pears.)Schust.
Cheilolejeunea krakakammae (Lindenb.) Schuster
Chiloscyphis muricatus (Lehm.) Engel & Schuster
Chiloscyphus cuspidatus (Nees) Engel & Schuster
Chiloscyphus difformis (Nees) Engel & Schuster
Dicranella subsubulata (C.Mnll.) Jaeg.
Dicranum johnstonii Mitt.
Diplasiolejeunea runssorensis Steph.
Donnellia matutina Buck
Entodon vulcanicus Demar. & Leroy
Evansiolejeunea roccatii (Gola)Vanden Berghen
Fissidens asplenioides Hedw.
Frullania arecae (Spreng.) Gott.
Frullania serrata Gott.
Funaria hygrometrica Hedw. var. *calvescens* Mont.
Hypnum cupressiforme Hedw.
Isopterygium mbangae (C. M ll.) Jaeg.
Isotachys aubertii (Schwaegr.) Mitt.

Jungermannia borgenii Gott. ex Steph.
Jungermannia sphaerocarpa Hook.
Lepidozia cupressina
Leptodontium viticulosoides (P.B.) Wijk & Marg.
Leptoscyphus hedbergii (Arnell) Schuster
Leptoscyphus infuscatus Mitt.
Lethocolea congesta (Lehm.) S.Arnell
Metzgeria agnewii Kuw.
Metzgeria australis Steph.
Metzgeria consanguinea Schiffn.
Metzgeria leptoneura Spr.
Metzgeria muscicola Steph.
Microlejeunea kamerunensis Steph.
Oreoweisia erosa
Palamocladium sericeum (Jaeg.) C. Müll.
Pilopogon africanus Broth.
Plagiochila corniculata (Dum.) Dum.
Plagiochila ericicola Mitt.
Plagiochila subalpina Steph.
Porotrichum molliculum Broth.
Radula voluta Tayl. ex Gott. & Lindenb.
Sphagnum planifolium C. Müll.
Sphagnum strictum Sull. ssp. *pappeanum*
Streptopogon erythrodontius (Tayl.) Wils.
Symphyogyna podophylla (Thunb.) Mont. & Nees
Tortula cavallii Negri
Trematodon intermedius Welw. & Duby
Trichosteleum pervilleanum (C. Müll.) Buck
Trichosteleum subulatulum (C. Müll.) Jaeg.

A wide range from the lowest to the highest altitudes within the transect have:
Calypogeia fissa (L.) Raddi
Campylopus pilifer Brid. (not below 1500 m)
Campylopus savannarum (C.Müll.) Mitt. (not above 2300 m)
Cephaloziella kiaerii (Aust.) Douin (1300 m - 2300 m)
Chiloscyphus muricatus (Lehm.) Engel & Schuster (1100 m - 3700 m)
Drepanolejeuna physaefolia (Gott.) Steph. (900 m - 3200 m)
Fissidens intramarginatus (Hampe) Mitt. (1500 m - 3200 m)
Fissidens laxus Sull. & Lesq. (1100 m - 2500 m)
Frullania obscurifolia Mitt. (1300 m - 2500 m)
Hypopterygium mildbraedii Broth. (1500 m - 2300 m)
Lejeunea flava (Sw.) Nees s.str. (850 m - 2700 m)
Lejeunea flavovirens Aongstr. (800 m - 3700 m)
Lejeunea isophylla E.W. Jones (900 m -2600 m)
Lejeunea ramosissima Steph. (850 m - 3240 m)
Metzgeria limbato-setosa Steph. in Mildbr. (900 m - 2600 m)
Philonotis falcata (Hook.) Mitt. (900 m - 3300 m)
Philonotis tomentella Lor. (1500 m - 3200 m)
Plagiochila divergens Steph. var. *myriocarpa* (1500 m- 2600 m)
Plagiochila fusifera Tayl.(1500 m - 2500 m)
Plagiochila integerrima Steph. (900 m - 2400 m)
Plagiochila pectinata (Willd.) Lindenb. (1300 m - 3200 m)
Plagiochila terebrans Ldbg. (1300 m - 3700 m)
Porothamnium stipitatum (Mitt.) Touw ex De Sloover (1100 m - 2400 m)
Radula holstiana Steph. (900 m - 2500 m)
Radula stipatiflora Steph. (1300 m - 3600 m)
Rhacopilopsis transvaaliensis (Thér. & Dix.) Buck (850 m - 2600 m)
Rhacopilopsis trinitensis (C. Müll.) Britt. & Dix. (1500 m- 2500 m)
Rhizogonium spiniforme (Hedw.) Bruch (1300 m - 2900 m)
Sphagnum davidii Warnst. (1300 m - 3400 m)
Syrrhopodon gardneri (Hook.) Schwaegr. (1300 m - 2300)
Syrrhopodon gaudichaudii Mont. (900 m - 2500 m)
Wijkia trichocolea (C. Müll.) Crum (900 m - 2500 m)

Floristic discontinuities were observed by Pócs (1991) at Mt. Kilimanjaro at 1800 m (lower limit of montane rainforest), 2500 m (lower limit of mossy forest) and 2800 m (beginning of *Erica* forest). These limits can be roughly compared with these at 2000 m, 2500 m and 3200 m in the BRYOTROP-transect.
In Peru, peak values of floristic discontinuities were found at 500 m, 1300 m, 1900 m, 2800 m and 3200 m (Gradstein & Frahm 1987). These

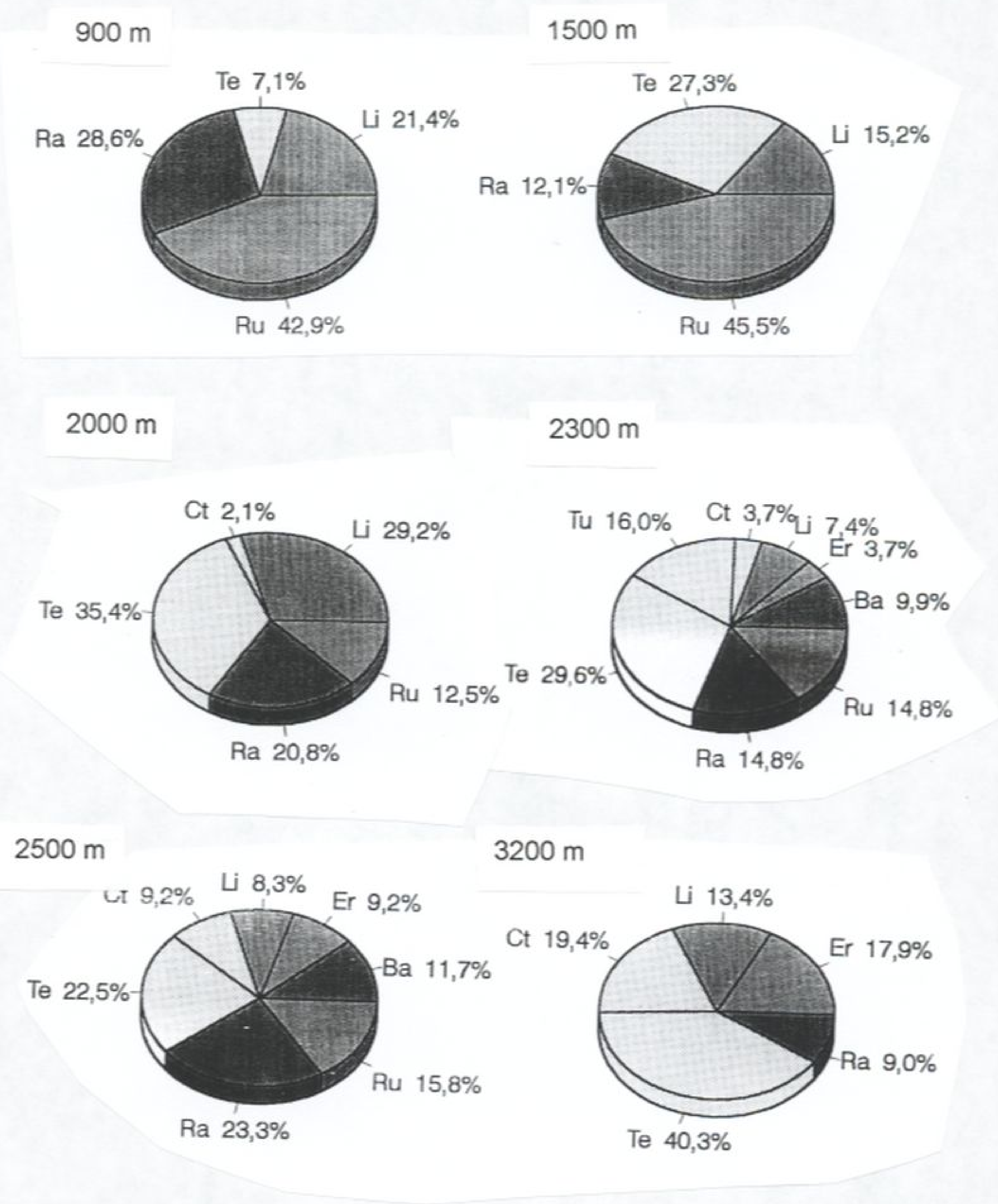

Fig. 6. Percentage of bryophytes on different substrates along the BRYOTROP transect in Zaire and Rwanda. (Ru = rupicolous, Te = terricolous, Ct = corticolous, Ra = ramicolous, Li = lignicolous, Tu = turficolous, Ba = on bamboo, Er = on ericaceous shrubs)

values also correspond well with the African transect at 1500 m, 2000 m and 3200 m. The only difference concerns the 2800 m discontinuity on the east slope of the Andes, which has no resemblences to the African transect.
In New Guinea, Enroth (1990) found floristic discontinuities at 300 m, 1200 m, 1500 m, 1800 m, 2500 m, 2800 m and 3400 m. The limits at 300 m, 1200 m, 1800 m, 2800 m and 3400 m correspond with the data obtained in Peru, those at 1500 m, 1800 m, 2500 m and 3400 m with the data obtained in Zaire and Rwanda. As Enroth demonstrated, there were no significant differences in the floristic discontinuities between mosses and hepatics and therefore no reason to treat them separately.
Unfortunately these results cannot be compared with the Mt. Kinabalu-transect in Borneo, since the floristic data (kept at the Botanical Museum in Berlin) are not available.

3. Ecological Zonation

The ecological zonation is based on the data for bryophyte cover and phytomass obtained for the ecological studies on the epiphytic bryophyte vegetation (for details see Frahm 1994). Bryophyte cover as well as phytomass of epiphytic bryophytes per 0,5m² and per hectare show lowest values between 900 and 1500 m altitude. Above 1500 m there is a sudden increase (Frahm 1994 figs. 3 and 7). Unfortunately, the exact location of the change could not be exactly defined, as the 1700 m relevée was omitted because there was no forest at this altitude in the transect. Highest values for cover are reached at 2300 m (resembling the "mossy forests" of the Andes or Mt. Kinabalu at the same elevation) and at the forest line at 3300 m. Between 2300 m and 3100 m, lower values are found as a consequence of small forest patches mixed in large bamboo stands.
For the first time the distribution of bryophytes on different substrates was evaluated along a BRYOTROP transect. For this purpose, the substrates were noticed in the field using the abbreviations based on a proposal by T. Pócs. Laterthe information was added to the database. By this way it could easily be determined, how many species were found in every altitude on various substrates.
The evaluation of these data revealed (fig. 6 shows data from 6 relevés from different altitudes), that only 7% of bryophytes were found on soil at 900m, but 27% at 1500 m, 35% at 2000 m, 29% at 2300 m, 22% at 2500 m and 40% at 3200 m. Thus terricolous species are increasing with the altitude, which is probably due to the higher light intensity at the forest floor. This would also explain the variation of the percentage of terricolous species between 2000 and 2500 m. Lignicolous species were represented with 21% at 900 m, 15% at 1500 m, 29% at 2000 m, but only 7% at 2300 m, 8% at 2500 m and 13% at 3200 m. The values show that about one fifth of species grows on this kind of substrtae in elevations below 2000 m. The decrease at higher altitudes may be due to the absence of suitable habitats in bamboo forests and ericaceous shrubs. The percentage of epiphytic species (ramicolous and corticolous species in fig. 6) varied between 28% at 900 m, 22% at 2000 m, 18% at 2300 m, 32% at 2500 m and 29% at 3200 m. Some habitats were only available at certain altitudes and cannot be compared through the whole transect. This concerns turficolous species at 2300 m, species growing on bamboo at 2300 m and 2500 m and on ericaceous shrubs at 3200 m.

4. Discussion

An integration of all methods used for determination of the altitudinal zonation of the rain forest along the Mt. Kahuzi transect in eastern Zaire (species per relevée, altitudinal ranges of species and phytomass of epihytic bryophytes) reveals the following limits:
Below 1500 m elevation, there are less than 40 species per hectare. A peak value of species numbers is found having their upper- or lowermost occurrence at this altitude. There are less than 20 g of epiphytic bryophytes per square meter or less than 20 kg per hectare.
Above 1500 m, there is a sudden increase in phytomass. At 2000 m, 40 species of bryophytes appear for the first time along the transect, raising the total number of species in a relevée

to 40-70. At 2600 m, 27 bryophyte species reach their uppermost elevation and are not found at higher altitudes. These species are replaced by others, raising the total number per relevée to more than 70. Most of these species are still found at 3200 m, where the highest value of phytomass of epiphytic bryophytes (6 to/ha) was recorded. Most of these species disappear above the forest line, resulting in a substantial decrease of species per relevée and phytomass per hectare.

Using the definitions for the altitudinal zonations of rain forests based on bryophytes proposed by Frahm & Gradstein (1991), the zone from 900 to 1500 m has to be classified as tropical submontane forest. Although tropical rain forests in other parts of the world (Peru, Colombia, Borneo) show a change from submontane to montane forests at elevations between 1300 and 1500 m, the change is situated higher in Eastern Zaire (between 1500 and 1900 m). The situation in Zaire at 1500 m resembles that at 1300 m on Mount Kinabalu or on the eastern slopes of the Andes. This is probably due to the drier climate of this region, which shifts the altitudinal belts upwards. Accordingly, the lower tropical montane forest ascends to 2100 m in the Mt. Kahuzi transect. Because of the predominant bamboo forests, the upper tropical montane forest in Central Africa is not as characteristic as in other parts of the tropics. It occurs from 2100 m to 2800 m in the Mt. Kahuzi-transect. At the forest line, the highest numbers of species and the highest values of epiphytic phytomass are found worldwide. This subalpine forest is situated on Mt. Kahuzi between 2900 and 3200 m. The summit region of Mt. Kahuzi belongs to the ericaceous belt above the forest line with a shrubby vegetation consisting of *Erica rugegensis* and giant *Senecios.* Due to the low elevation of the summit of Mt. Kahuzi (3300 m), the upper vegetation belts are comparably lower than elsewhere. This is also the case with Mt. Biega, which is even lower (2900 m) . In contrast, the altitudinal belt on Mt. Karismbi (4500 m) are situated accordingly higher.

Except for a different terminology, the altitudinal zonation based on floristic and ecological paramaters derived from bryophytes resembles that of Hamilton (1982). The submontane forest and the lower montane forest of the present study is referred to as evergreen lowland forest by Hamilton (1982). The term "lowland" is not very appropriate for elevations as high as 1900 or 2000 m, especially as true lowland forest is found at lower latitudes (e.g. in the Zaire basin), which is not covered in the scheme of Hamilton.

The upper montane forest of the present study is referred to by Hamilton (1982) as moist lower montane forest, and the upper montane forest of the present study as bamboo zone. The bamboo zone is a vegetation belt typical for tropical Africa but has no similar occurrence elsewhere in the world. Therefore, from a globar perspective, the bamboo forest can be regarded as an African expression of the lower part of the upper montane forest. The subalpine forest in this study is referred to by Hamilton (1982) as upper montane forest. In both schemes, the ericaceous belt occurs above the forest line on mountains presumably with acidic rocks, such as Mt. Kahuzi, but not volcanoes with basic lava flows e.g. Mt. Karisimbi, where *Hypericum - Senecio - Lobelia* stands replace the ericaceous belt. The ericaceous belt in Hamilton´s scheme is situated between 3400 - 3600 m, which is broadly correct, but does not take into account the situation oon lower mountains such as Mt. Kahuzi.

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Literature

Enroth, J. 1990. Altitudinal Zonation of Bryophytes on the Huon Peninsula, Papua New Guinea. Tropical Bryology 2: 61-90.

Fischer, E. 1993. Taxonomic Results of the BRYOTROP Expedition to Zaire and Rwanda 3. Description of Collecting Sites. The Vegetation of Kahuzi-Biega National Park/Zaire, Nungwe Forest/Rwanda and Virunga volcanoes/Rwanda. Tropical Bryology 8:

13-38.

Frahm, J.-P. 1990a. The altitudinal zonation of bryophytes on Mt. Kinabalu. Nova Hedwigia 51: 133-149.

Frahm, J.-P. 1990b. Bryophyte phytomass in tropical ecosystems. Botanical Journal of the Linnean Society 104: 23-33.

Frahm, J.-P. 1994. Scientific Results of the BRYOTROP Expedition to Zaire and Rwanda 17. Andreaeaceae, Bruchiaceae, Dicranaceae, Rhizogonuaceae, Bartramiaceae, Rhacocarpaceae, Hedwigiaceae, Cryphaeaceae, Leucodontaceae. Tropical Bryology 8: 153-170.

Frahm. J.-P. & Gradstein, S.R. 1991. An altitudinal zonation of tropical rain forests using bryophytes. Journal of Biogeography 18: 669-678.

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.

Gradstein, S.R. & Frahm, J.-P. 1987. Die floristische Höhengliederung der Moose entlang des Bryotrop Transekt in NO-Peru. Beih. Nova Hedwigia 88: 105-114.

Gentry, A.H. 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? Ann. Miss. Bot. Garden 69(3): 557-593.

Hamilton, A. 1982. Environmental History of East Africa. New York (Academic Press).

Hamilton, A. 1989. African forests. Pp. 155-182 in H. Lieth & M.J.A. Werger (eds.) Tropical Rain Forest Ecosystems. Ecosystems of the world vol. 14B. Elsevier, Amsterdam.

Hedberg, O. 1951. Vegetation belts of the East African mountains. Svensk Bot. Tidskrift 45(1): 140-202.

Kürschner, H. 1990. Höhengliederung (Ordination) von epiphytischen Laub- und Lebermoosen in Nord-Borneo (Mt. Kinabalu). Nova Hedwigia 51: 77-86.

Pócs, T. 1991. The altitudinal distribution of Kilimanjaro bryophytes. Abstract, AEFTAT Conference, Malawi.

Reenen, G.B.A. van & Gradstein, S.R. 1984. An investigation of bryophyte distribution and ecology along an altitudinal gradient in the Andes of Colombia. J. Hattori Bot. Lab. 56: 79-84,

Sipman, H.J.M. & Harris, R.C. 1989. Lichens. Pp. 303-310 in H. Lieth & M.J.A. Werger (eds.) Tropical Rain Forest Ecosystems. Ecosystems of the world vol. 14B. Elsevier, Amsterdam.

Tryon, R. 1989. Pteridophytes. Pp. 327-338 in H. Lieth & M.J.A. Werger (eds.) Tropical Rain Forest Ecosystems. Ecosystems of the world vol. 14B. Elsevier, Amsterdam.