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Scientific results of the BRYOTROP expedition to Zaire and Rwanda

7. Life strategies of epiphytic bryophytes from tropical lowland and montane forests, ericaceous woodlands and the *Dendrosenecio* subpáramo of the eastern Congo basin and the adjacent mountains (Parc National de Kahuzi-Biega/Zaire, Forêt de Nyungwe/Rwanda)

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Abstract: Life strategies of epiphytic bryophytes are studied along an altitudinal gradient from the eastern Congo basin (tropical lowland zone) to the mountains of the East-African graben (tropical subalpine/alpine Zone; BRYOTROP III-transect). Three strategies, Colonists, Perennial shuttle species and Perennial stayers can be observed, which are further subdivided according to their reproduction tactic (high sexual reproductive effort, high asexual reproductive effort, moderately or low sexual and asexual reproductive effort). Of these, only taxa with a long life span (perennials) are of importance, indicating the unchanging and constant ecological conditions and long-lasting microsites, provided by the epiphytic habitats.

The basis for the life strategy pattern analysis along the altitudinal gradient were plant sociological investigations and the determination of the mean percentage cover values for the different life strategy categories. By this, the distribution and occurrence of the different strategies within the communities and the altitudinal zones can be shown.

Typical for the epiphytes of the primary rain-forests of the tropical lowland and lower montane zone are Perennial shuttle species and Perennial stayers with moderately or low sexual and asexual reproductive effort. This strategy obviously is favoured by the well balanced, high temperature and humidity regime of these zones and typical of most of the liverworts, dominating the epiphytic communities. They are replaced in the montane rain-forests and cloudy moss forests of the upper tropical montane zone by Perennial shuttle species with high asexual reproductive effort, regenerating mainly by propagules and clonal growth. Within the secondary woodlands of this zone and the unique ericaceous woodlands and subpáramo of the African volcanos, Perennial shuttle species and Perennial stayers with high sexual reproductive effort reach a maximum, building regularly sporophytes under the already xeric and strong diurnal climatic conditions of the subalpine/alpine zone. This reproduction strategy is typical of epiphytic communities of xerophytic woodlands. The frequent change within the life strategy spectra of the different altitudinal zones indicates, that life strategies can be seen as a set of co-evolved adaptive traits, which grow and evolve within different taxa under similar ecological conditions.

Zusammenfassung: Aufbauend auf einer pflanzensoziologischen Analyse wurden die Lebensstrategien epiphytischer Bryophyten entlang eines Höhenstufentranssektes im östlichen Kongobecken (Tieflandstufe) bis zum zentralafrikanischen Grabenrand (tropisch subalpine/alpine Stufe; BRYOTROP III-Transsekt) aufgezeigt und in Beziehung zu den verschiedenen Moosgesellschaften und dem ökologischen Gradienten gesetzt. Grundlage für die Interpretation ist der mittlere Gruppenmengenanteil. Drei Lebensstrategien, Besiedler (Colonists), Ausdauernde Pendler (Perennial shuttle species) und Ausdauernde (Perennial stayers) können unterschieden werden, die aufgrund ihres Reproduktionsverhaltens [hohe generative Reproduktion, hohe vegetative Reproduktion, niedere generative und vegetative (passive) Reproduktion] weiter unterteilt werden können. Von diesen erreichen nur die beiden Strategien, die durch langlebige (perennierende) Sippen gekennzeichnet sind, hohe Wertigkeiten in den Gesellschaften. Dies deutet auf konstante Umweltbedingungen und für lange Zeit verfügbare Mikronischen hin. Kennzeichnend für die Epiphytengesellschaften primärer Regenwälder der tropischen Tiefland- und der unteren Bergwaldstufe sind Ausdauernde Pendler und Ausdauernde mit passivem Reproduktionsverhalten. Dieses Reproduktionsverhalten wird durch die sehr ausgeglichenen hohen Temperatur- und Luftfeuchtigkeitsverhältnisse in dieser Stufe gefördert und ist typisch für die meisten der in diesen Epiphytengesellschaften dominierenden Lebermoose. Im tropischen Bergregen- und Nebelwald der oberen montanen Stufe wird diese passive Strategie durch Ausdauernde Pendler mit vegetativem Reproduktionsverhalten ersetzt, die sich v.a. aus vegetativ gebildeten Diasporen und einem ausgeprägten klonalen Wachstum regenerieren. Innerhalb der sekundären, offenen Bergwälder dieser Höhenstufe und in den auf die zentralafrikanischen Vulkane beschränkten Heidebuschwäldern und der Subpáramo-Vegetation erreichen Laubmoose mit der Lebensstrategie Ausdauernde Pendler und Ausdauernde mit generativem Reproduktionsverhalten hohe Anteile. Sie bilden in der bereits trockeneren und durch Frostwechselklima gekennzeichneten subalpinen/alpinen Höhenstufe regelmäßig Sporogone und vermitteln mit dieser Strategie bereits zu den Epiphytengesellschaften xerophytischer Offenwälder. Dieser auffallende Wechsel im Lebensstrategienspektrum entlang des Höhenstufengradienten zeigt, daß Lebensstrategien einen Komplex gemeinsam erworbener Anpassungsmerkmale darstellen, die sich unter ähnlichen bzw. gleichen Umweltbedingungen herausbilden.

Introduction

Life strategies in bryophytes can be envisaged as a system of co-evolved adaptive traits (Stearns 1976, During 1979, 1992, Frey & Kürschner 1991a) implying numerous adaptations to the environmental conditions. Their classification can be very useful for making comparisons of the ecology of species and communities in different habitat sites and geographical regions. A general concept of a life strategy system to bryophytes has been applied by During (1979), consisting of six life strategy categories (Annual shuttle species, Fugitives, Colonists, Short lived shuttle species, Perennial shuttle species, Perennial stayers, Tab. 1). It is based on several characters, among which life span, reproductive effort [potential life span of the gametophyte, which is negatively correlated with the reproductive effort; avoidance strategy (discarding the gametophyte, and survival of the difficult season as spores only) versus tolerance strategy (survival of the gametophyte)] and dispersal mechanisms (few large spores with decreasing long-distance dispersal versus many small spores with chance dispersal) are of great importance (During 1979, 1992). This provisional system was further subdivided by Frey & Kürschner (1991a) with respect to the dominating reproductive tactic and completed by a seventh category, the geophyte life strategy (Tab. 1).

Despite of often incompletely known aspects like life history, the importance and potential adaptive value of asexual reproduction (clonal growth and propagules) and the dispersal capacity of the diaspores, within the last years different bryophyte communities of various habitat sites and geographical regions have been analyzed (During 1981, During & ter Horst 1985, Frey & Kürschner 1991a,b,c, 1995a,b, Kürschner 1994) demonstrating key factors and interactions between plants, communities and environment.

With this study, for the second time we present an analysis of life strategies of tropical epiphytic bryophytes and their life strategy distribution pattern along an altitudinal gradient of the tropics (eastern Congo basin and adjacent mountains, BRYOTROP III-transect).

Material and methods

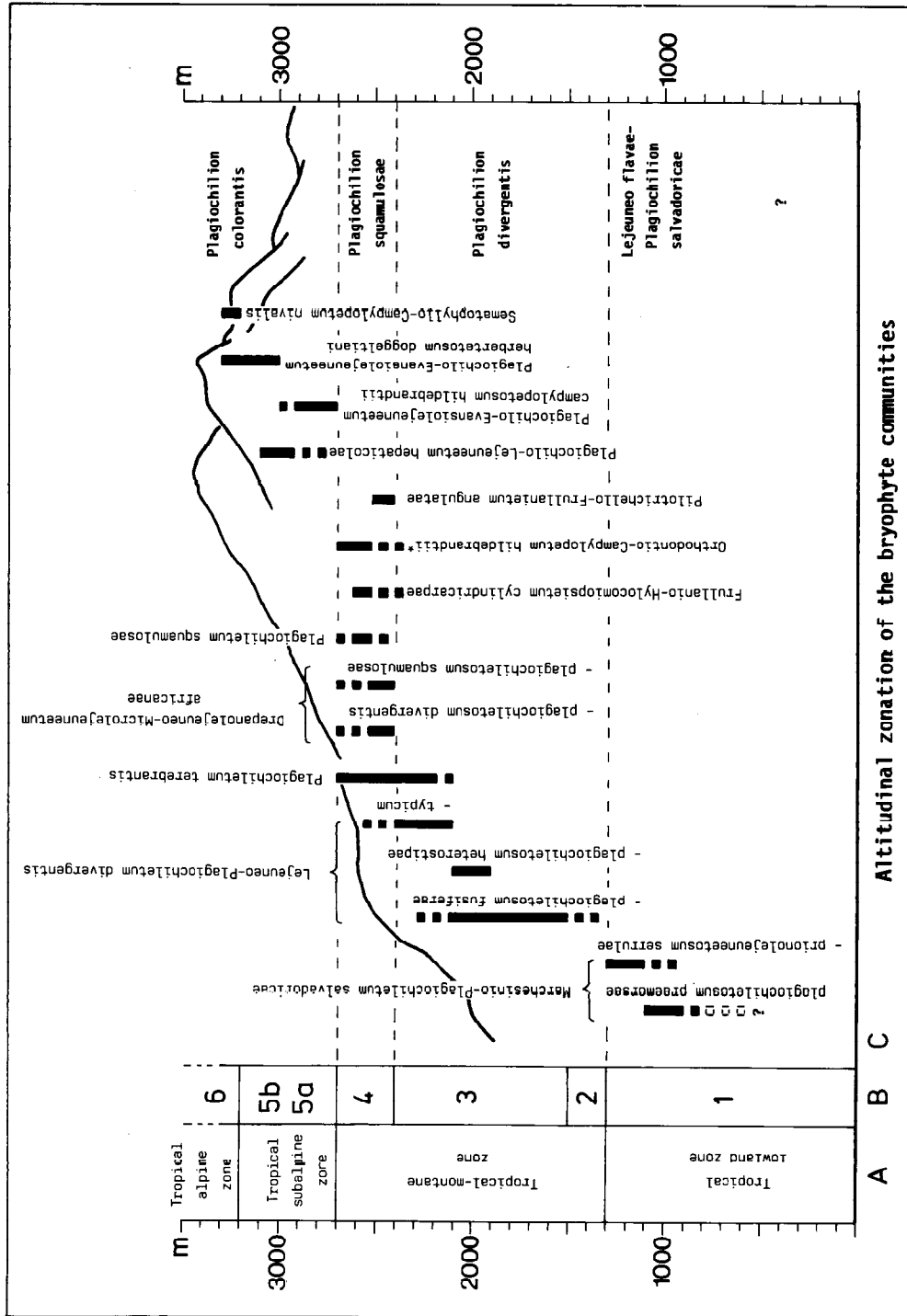
The life strategy analysis of the epiphytic bryophytes (shade epiphyte synusia) is based on a plant sociological analysis (Kürschner 1995a), which was carried out along an altitudinal gradient from the eastern Congo basin [Irangi (850)-900 m, upper tropical lowland zone] to the mountains of the East-African graben [Mt. Biega (2790 m), Mt. Kahuzi (3308 m), tropical subalpine/alpine zone; BRYOTROP III-transect]. Within this altitudinal gradient, comprising the upper tropical lowland zone (Caesalpiniaceae lowland forests, Pluviisilvae Klötzli 1958, forêt ombrophile Prioul & Sirven 1981), the lower and upper tropical montane zone (montane rain-forests, Laurisilvae, forêt ombrophile de montagne and bamboo-forests), the tropical subalpine zone (ericaceous woodlands, Ericifruticeta, étage des bruyères) and the tropical alpine zone (*Dendrosenecio*-subpáramo, Frigidideserta), 11 associations and 9 subassociations occur (Fig. 1), which synhierarchically can be classified into 4 alliances. The vertical distribution of these 4 alliances corresponds well with the altitudinal zonation at the eastern Congo basin, the distribution of the different forest types, as well as the ordination of the different bryophytes (ecological groups, Kürschner 1995b) characterizing the transect.

For the analysis itself, the plant material collected during the field trip, older collections from Central Africa (B) and some few data from literature (Correns 1899, Fleischer 1900-1922, Schuster 1988) were available. Data concerning the asexual and sexual reproductive effort often were sparse, thus making the classification to the different life strategy categories more difficult. The quantitative calculation of the life strategy spectra is based on the mean percentage cover value of each species and category (Frey & Kürschner 1991a,b) within the different altitudinal zones and the different bryophyte associations. By this, the biological relevance of each life strategy within the entire spectrum, as well as the different life strategy patterns of each zone can be shown, which are strongly related to and influenced by the ecological gradient.

	Life span				Reproduction				Innovations		Distribution of gametangia		
	ephemeral, winter annual, summer annual	pauciennial	perennial	with subterranean stems	Sexual reproduction	Spores	Asexual reproduction			monocious	dioctious		
Annual shuttle species Einhährige Pendler	●				●	●	●		●				P _o
Fugitives Kurzlebige	●				●		●		●				K
Colonists Besiedler	Colonists with high sexual reproductive effort	●				●	●		●				B _g
	Colonists with high asexual reproductive effort	●					●	●	●				B _v
	Colonists with sexual and asexual reproductive effort	●				●	●		●				B _{v,g}
	Colonists with basicline innovations	●				●	●			●			B _i
	Pauciennial colonists		●			●	●		●				B _a
Short lived shuttle species Kurzlebige Pendler		●			●	●		●					P _k
Perennial shuttle species Ausdauernde Pendler	Perennial shuttle species with high sexual reproductive effort		●			●	●		●				P _g
	Perennial shuttle species with high asexual reproductive effort		●				●	●	●				P _v
	Perennial shuttle species with sexual and asexual reproductive effort		●			●	●		●				P _{v,g}
	Perennial shuttle species with moderately or low sexual and asexual reproductive effort		●				●	●	●				P _p
Perennial stayers Ausdauernde	Perennial stayers with high sexual reproductive effort		●			●	●		●				A _g
	Perennial stayers with high asexual reproductive effort		●				●		●				A _v
	Perennial stayers with moderately or low sexual and asexual reproductive effort		●				●	●	●				A _p
Geophyte Geophyt			●	●		●		●		●			Geo

Tab. 1. Life strategy categories of bryophytes (after During 1979, Frey & Kürschner 1991a).

Fig. 1. (p. 133) Zonation of epiphytic bryophyte communities (C) in eastern Zaire (Mt. Biega, Mt. Kahuzi) and Rwanda (Forêt de Nyungwe). [A altitudinal zonation; B forest formations (cf. Hedberg 1951, Klötzli 1958, Prioul & Sirven 1981; 1 Caesalpinaceae lowland forests, forêt ombrophile, Pluviisilvae; 2 *Julbernardia-Ocotea* transition forest, forêt de transition; 3 montane rain-forest, forêt ombrophile de montagne, Laurisilvae; 4 bamboo-forest, étage à *Arundinaria alpina*; 5a *Podocarpus-Syzygium-Psychotria* forest; 5b ericaceous woodlands, étage à bruyères, Ericifruticeta; 6 *Dendrosenecio*-subpáramo, páramo à *Senecio et Lobelia*, Frigidideserta. * synhierarchical position uncertain]. (After Kürschner 1995a).



Results and discussion (Tab. 2-4, Figs. 2-5)

The epiphytic bryophytes of the BRYOTROP III-transect (Parc National de Kahuzi-Biega/Zaire, Forêt de Nyungwe/Rwanda), together with their main characters (e.g. life form, sexual and asexual reproductive effort, dispersal strategy, distribution of gametangia and life strategy) are listed in Tab. 2. Altogether, only three categories of life strategies, Colonists (3 taxa), Perennial shuttle species (48 taxa), Perennial stayers (99 taxa) occur, indicating the more or less stable ecological conditions within the different epiphytic bryophyte communities of each altitudinal zone.

1. Colonists

Species with the Colonists' strategy are characterized by a moderately short life span of only a few years (pauciennial-pluriennial taxa), a high sexual and/or asexual reproductive effort, small spores (less than 25 μm) indicating long-range dispersal with spores and short-range dispersal with asexual diaspores. In tropical epiphytic communities, taxa with this life strategy consist of truly colonizing species with a pioneer-character, appearing in early succession series or mainly disturbed communities (Frey & Kürschner 1991b). In the transect analyzed, this strategy is confined to the tropical lowland (900 m) and tropical montane zone (1900 m, 2300 m, Tab. 3), but reaching here only very low mean percentage cover values (less than 1%). According to the reproductive tactic, the Colonists can be subdivided into Colonists with asexual and sexual reproductive effort ($B_{v,g}$; only *Octoblepharum albidum*), Colonists with high sexual reproductive effort (B_g ; only *Aneura pseudopinguis*) and Colonists with high asexual reproductive effort (B_v ; only *Syrrhopodon gardneri*), all being of less importance within the life strategy spectra and their distribution pattern (the Colonists' strategy is not shown in a separate figure).

2. Perennial shuttle species

The life strategy Perennial shuttle species comprises taxa with a long life span (pluriennial-perennial taxa), a moderate, sometimes low to absent or high sexual and/or asexual reproductive effort, a normally rather high age of first sexual reproduction (more than 5 years), and rather large spores (> 25

μm) in regularly sporulating species. In accordance with During (1979), Frey & Kürschner (1991a,c), Miles & Longton (1992) and Stoneburner et al. (1992), the probable dispersal distance rapidly decreases by spores larger than 25 μm , indicating short-range dispersal and an atelechorous tendency. This, and the relatively high number of taxa belonging to this strategy (48 taxa, Tab. 1) is in contrast to Grime et al. (1990), who postulate small spores with long-range dispersal as an important regeneration strategy of epiphytic bryophytes. The Perennial shuttle strategy is typical of unchanging and constant ecological conditions and long-lasting microsites, as it is provided by many epiphytic habitats.

The further subdivision of the category clearly shows an altitudinal zonation (Fig. 2), which is reflected also by the different proportions within the ecological groups (Fig. 4) and the different proportions within the epiphytic communities (Fig. 5).

The epiphytic communities of the tropical lowland zone (Caesalpiniaceae lowland forests and *Julbernardia-Ocotea* transition forest) are dominated by species of the life strategy Perennial shuttle species with moderately or low sexual and asexual reproductive effort (P_p , Tab. 3, Fig. 2). Most of the species characterizing syntaxonomically the Marchesinio-Plagiochiletum salvadoricae and the Lejeuneo-Plagiochiletum divergentis plagiochiletosum fusiferae, like *Marchesinia excavata*, *M. moelleriana*, *Plagiochila fusifera*, *P. salvadorica*, *Porella subdentata*, *Radula appressa*, *R. boryana* and *Syrrhopodon armatus* belong to this strategy, showing a low or nearly absent asexual and sexual reproduction. Their dominance on the phorophyte and within the epiphytic communities mainly is a result of clonal growth of the often unisexual populations (dioecious species), which is supported by the balanced climatological conditions (isothermie, high and stable humidity) of this altitudinal zone. In contrast, Perennial shuttle species with high sexual reproductive effort (P_g) reach their maximum within the epiphytic communities of the upper tropical montane zone (montane rain-forests and bamboo-forests, Tab. 3, Fig. 2). This strategy is typical for *Plagiochila divergens* and *P. squamulosa*, the leading species of the Lejeuneo-Plagiochiletum divergentis typicum, the

Plagiochiletum squamulosae and the two subassociations of the Drepanolejeuneo-Microlejeuneetum africanae of the primary rain-forests of this zone (Tab. 4, Fig. 5). Also various mosses like *Brachymerium nepalense*, *B. rigidum*, *Hylocomiopsis cylindricarpa*, *Neckera platyantha*, *N. remota*, *Macrocoma abyssinica* and *Syrhropodon incompletus* fall into this category, which is typical of the more or less open, secondary montane forests (*Nuxia floribunda*-*Agauria salicifolia* community, *Hagenia abyssinica* fragments), dominated by the Frullanio-Hylocomiopsietum cylindricarpae (Tab. 4, Fig. 5). Obviously, the more open and already xeric conditions in these forests favoured regularly sporulating species. Their relatively large spores have a low dispersal capacity, but probably better chances of successful establishment and a longer life span in the diaspore bank (During 1992).

Perennial shuttle species with high asexual reproductive effort (P_v) mainly are restricted to the tropical subalpine/alpine zone (*Podocarpus-Syzygium-Psychotria* forest and ericaceous woodlands, Tab. 3, Fig. 2). In contrast to the previous category, the sexual reproduction in this group is low to absent, but asexual diaspores (mainly flagellae, gemmae, breaking-off of leaf tips and shoots) are regularly produced in large amounts. To this strategy, some of the most conspicuous afro-alpine epiphytes belong, e.g. *Anastrophyllum auritum*, *Andrewsianthus bilobus*, *Herbertus doggeltianus*, *H. lobatus* or *Plagiochila barteri* ssp. *colorans*, which are typical components of the humid Plagiochilo-Lejeuneetum hepaticolae and the Plagiochilo-Evansiolejeuneetum roccatii (Tab. 4, Fig. 5). This group shows a strong tendency towards reduced sporophyte production and increased reliance on asexual propagules for population maintenance.

3. Perennial stayers

As in the Perennial shuttle strategy, the life strategy Perennial stayers also is characterized by species with a long life span (perennial taxa), but in contrast to the shuttle strategy, the spores are small (less than 25 μm) and long-range as well as short-range dispersal is possible (chance dispersal). This strategy is typical of most of the epiphytic species analyzed in the transect (99 taxa, Tab. 1) and most frequent in later successional and

climax stages (permanent habitats).

Two species, *Metzgeria australis* and *Plagiochila terebrans* belong to the Perennial stayers with high sexual and asexual reproductive effort ($A_{g,v}$, Tab. 2). Their mean cover percentage value within the life strategy spectra normally is low (Fig. 3), except in the tropical montane zone (montane rain-forests), where this strategy reaches a high value in the Plagiochiletum terebrantis (Tab. 4, Fig. 5), due to the high cover abundance of *Plagiochila terebrans*.

Perennial stayers with high sexual reproductive effort (A_g) reach higher maxima especially in the more xerophytic, secondary woodlands of the upper tropical montane zone and in the tropical subalpine/alpine zone. Various mosses like *Brachymerium speirocladum*, *Campylopus hildebrandtii*, *C. nivalis*, *Chrysohypnum frondosum*, *Hypnum cupressiforme* var. *townsendii*, *Leptodontium viticulosoides*, *Orthodontium gracile*, *Pyrrhobryum spiniforme* or *Sematophyllum stylites* belong to this strategy, which is highly dominant in the Frullanio-Hylocomiopsietum cylindricarpae and the Orthodontio-Campylopetum hildebrandtii of the *Nuxia floribunda*-*Agauria salicifolia* woodlands and the *Hagenia abyssinica* fragments, as well as in the Sematophyllo-Campylopetum nivalis of the *Dendrosenecio* subpáramo (Tab. 4, Fig. 5). These mosses sporulate regularly, but the age of the first reproduction is variable, taking at least several years. The small spores often are produced in large numbers, to make sure that many of them will reach the distant phorophytes and seem to serve for the occasional establishment of new populations. Within the liverworts, *Lejeunea confusa*, *L. flava*, *L. helenae*, *L. tabularis* and *Metzgeria consanguinea* show this strategy, and therefore have a wider distribution within the communities and along the altitudinal gradient. In general, this strategy is typical of epiphytic communities of more open, xeric sites and woodlands with high light intensities and a high diurnal variation of temperature and humidity (Frey & Kürschner 1995a). In the transect, one can observe an increasing number of Perennial stayers characterized by regularly sporulating species in higher altitudes and already xeric woodlands.

Perennial stayers with high asexual reproductive effort (A_v) by means of flagellae, stoloniferous

	Life-form	Sexual diaspores			Monoecious/dioecious	Sexual reproduction	Spores (ϕ in μ m)	Asexual diaspores			Asexual reproduction	Others	Life-strategy
		Relevé	Other samples	Literature				Relevé	Other samples	Literature			
Hepaticae													
Adelanthaceae													
Adelanthus decipiens	Ma	-	-	+	D	a	(23-30)	+	-	fD	h	F1	A _v
Adelanthus lindenbergianus	tT	-	-	+	D	a	(12-16)	-	-	[Ge]	e		A _p
Aneuraceae													
Aneura pseudopinguis	Ma	+	-	-	M	h	13-16	Ge	-	-	l		B _g
Riccardia amazonica	Ma	+	-	-	D	a,l		-	-	-	a		A _p
Riccardia compacta	Ma	+	-	-	M,D	a,l	12-22	[Ge]	-	-	l,m		A _v
Calypogeiaceae													
Calypogeia fissa	Ma	-	-	+	Mat	l,m	8-17	-	-	fD,Ge	l		A _g
Geocalyceae													
Chiloscyphus cuspidatus	Ma	+	-	+	Mat	h	14-16	-	-	-	a		A _g
Chiloscyphus difformis	Ma	+	-	-	D	a,l		[B1],Bs	-	-	a,l		A _p
Chiloscyphus fragrans	Ma	-	-	+	Mat	e		-	-	-	a		A _p
Chiloscyphus martianus	Ma	-	-	-		e		-	-	-	e		A _p
Chiloscyphus muricatus	Ma	+	-	-	M	a,l		+	-	-	l,m	F1	A _v
Leptoscyphus infuscatus	Ma	-	-	+	D	e		+	-	-	a,l	F1	A _p
Herbertaceae													
Herbertus dicranus	We	-	-	+	(D)	a		fD	-	-	m	F1	P _v
Herbertus doggeltianus	tT	-	-	+	D	a		fD	-	-	l,m	F1	P _v
Herbertus lobatus	tT	-	-	+	D	a		fD	-	-	m	F1	P _v
Herbertus subdentatus	We	-	-	+	D	a		fD	-	-	h	F1	P _v
Jubulaceae													
Frullania angulata	Pe	+	-	+	D	m	(40-50)	-	-	-	a		P _p
Frullania apicalis	Ma	+	-	+	D	a,l	(40-50)	B1	-	B1	m		P _v
Frullania arecae	Ma	+	-	+	Mat	m	(40-50)	-	-	-	a		P _g
Frullania depressa	Ma	+	-	+	Mat	h	(40-50)	-	-	-	a		P _g
Frullania ericoides	Ma	-	-	+	D	a	(40-50)	-	-	Ge	l		P _p
Frullania obscurifolia	Ma	+	-	+	D	a,l	(40-50)	-	-	Ge	l		P _p
Frullania serrata	Ma	+	-	+	M	m	(40-50)	-	-	-	a		P _g
Frullania variegata	Ma	+	-	+	D	m	(40-50)	B1	-	-	m		P _v
Jungermanniaceae													
Anastrophyllum auritum	We	-	-	-		a		B1,Bs	-	-	h	F1	A _v /P _v
Andrewsianthus bilobus	We	-	-	-		a		B1,fD	-	-	h	F1	P _v
Chandonanthus hirtellus	tT	-	-	-	D	a		-	-	-	[a]	[Bs]	A _p /P _v
Lejeuneaceae													
Aphanolejeunea exigua var. exigua	Ma	-	-	+	D,M	a		-	-	Ge	l		A _p
Cheilolejeunea krakammae	Ma	-	-	+	D	l		Ge	-	-	a,l		A _p
Cheilolejeunea pluriplicata	Ma	+	-	+	M	a,l		-	-	-	a		A _p
Cololejeunea zenkeri	Ma	-	-	+	M	a		-	-	Ge	l		A _p

<i>Diplasiolejeunea cornuta</i>	Ma	+	-	+	M	l		-	-	Ge	l		A _p
<i>Diplasiolejeunea kraussiana</i>	Ma	-	-	+	M	a		-	-	Ge	l		A _p
<i>Diplasiolejeunea runsaorensis</i>	Ma	+	-	+	D	a,l		Ge	-	Ge	m		A _v
<i>Drepanolejeunea physaefolia</i>	Ma	+	-	+	D	a		Bs	-	-	h		A _v
<i>Evansiolejeunea roccatii</i>	We	+	-	+	D	a		[B1]	-	-	a	[F1]	A _p
<i>Lejeunea caespitosa</i>	Ma	-	-	+	D	a		-	-	B1,Ge	l		A _p
<i>Lejeunea capensis</i>	Ma	-	-	+	D	a		-	-	-	a		A _p
<i>Lejeunea confusa</i>	Ma	+	-	+	D	l,m		-	-	-	a		A _p
<i>Lejeunea cysthearum</i>	Ma	+	-	+	Mat	m		-	-	-	a		A _g
<i>Lejeunea eckloniana</i>	Ma	[+]	-	+	Mat	h		-	-	-	a		A _g
<i>Lejeunea flava</i>	Ma	+	-	+	Mat	h	14	-	-	-	a		A _g
<i>Lejeunea flavovirens</i>	Ma	-	-	+	M	a		-	-	-	a		A _p
<i>Lejeunea helenae</i>	Ma	-	-	+	D	a		-	-	[Bs]	a		A _p
<i>Lejeunea hepaticola</i>	Ma	+	-	+	M,D	m		-	-	-	a		A _g
<i>Lejeunea isophylla</i>	Ma	+	-	+	D	a		-	-	-	a		A _p
<i>Lejeunea tabularis</i>	Ma	+	-	+	M	m		-	-	-	a		A _g
<i>Leucolejeunea xanthocarpa</i>	Ma	+	-	+	Mat	[m]		-	-	-	a		A _p
<i>Lopholejeunea spec.</i>	Ma	-	-	-	e			-	-	-	a		A _p
<i>Marchesinia excavata</i>	Ma	-	-	+	D	a	(35-40)	-	-	-	a		P _p
<i>Marchesinia muelleriana</i>	Ma	-	-	+	M	a	(35-40)	-	-	-	a		P _p
<i>Microlejeunea africana</i>	Ma	+	-	+	D	a,l		+	-	-	l	[F1]	A _p
<i>Microlejeunea kamerunensis</i>	Ma	+	-	+	D	m,h		+	-	-	o		A _g
<i>Prionolejeunea serrula</i>	Ma	-	-	+	M	a		-	-	-	a		A _p
<i>Ptychanthus striatus</i>	Ma	+	-	-	D	a,l		-	-	-	a		A _p
<i>Rectolejeunea rhodesiae</i>	Ma	+	-	+	D	a,l		B1,FD	-	B1	l,m	F1	A _v
<i>Schiffnerolejeunea altimontana</i>	Ma	+	-	-	D	a		[B1]	-	-	a,l		A _p
Lepidoziaceae													
<i>Bazzania decrescens</i>	We	+	-	+	D	a,l	(15-20)	B1	-	+	l	[F1]	A _p
<i>Bazzania pumila</i>	Ma	-	-	+	D	a	(15-20)	B1	-	+	l	[F1]	A _v
<i>Bazzania roccatii</i>	We	-	-	+	D	a	(15-20)	B1	-	+	h	[F1]	A _v
<i>Lepidozia cupressina</i>	We	-	-	+	D	a	(11-15)	Bs,FD	-	+	h		A _v
<i>Lepidozia stuhlmannii</i>	We	-	-	+	D	a	(11-15)	Bs,FD	-	+	l		A _p
Metzgeriaceae													
<i>Metzgeria australis</i>	Ma	+	-	+	D	l,m	16-24	Ge	-	Ge	h		A _{g,v}
<i>Metzgeria consanguinea</i>	Ma	+	-	+	D	l,h	20-26	+	-	-	l	aT	A _g
<i>Metzgeria leptoneura</i>	Ma	+	-	+	D	a,l	15-24	+	-	+	l	aT	A _p
<i>Metzgeria limbato-setosa</i>	Ma	-	-	+	D	a	(>30)	+	-	-	m	aT	P _v
<i>Metzgeria musicola</i>	Ma	-	-	-	e		(>30)	+	-	-	h	aT	P _v
Plagiochilaceae													
<i>Plagiochila barberi</i> ssp. <i>colorens</i>	Fa	-	-	+	D	a,h	(15-28)	B1	-	B1	m		P _v
<i>Plagiochila corniculata</i>	Ma	-	-	+	D	a	(15-28)	B1,FD	-	B1,FD	h		P _v
<i>Plagiochila divergens</i> var. <i>divergens</i>	Fa	+	-	+	D	h	(15-28)	-	-	[+]	a		P _g
<i>Plagiochila divergens</i> var. <i>myriocerpa</i>	Fa	+	-	+	D	a,l	(15-28)	[B1],FD	-	[+]	a,l	F1	P _g
<i>Plagiochila ericicola</i>	Fa	-	-	-	D	a	(15-28)	-	-	-	a		P _p
<i>Plagiochila fusifera</i>	Fa	+	-	+	D	a	(15-28)	FD	-	B1	l		P _p

	Life-form	Sexual diaspores			Monoecious/dioecious	Sexual reproduction	Spores (Ø in µm)	Asexual diaspores			Asexual reproduction
		Relève	Other samples	Literature				Relève	Other samples	Literature	
<i>Plagiochila heterostipe</i>	Fa	-	-	-		a	15-22	-	-	-	a
<i>Plagiochila integerrima</i>	Fa	-	-	-		a	(15-28)	-	-	-	[1]
<i>Plagiochila praemorsa</i>	Fa	-	-	+	D	a	(15-28)	-	-	-	a
<i>Plagiochila salvadorica</i>	Fa	+	-	+	D	l	(15-28)	-	-	Ge	a,l
<i>Plagiochila squamulosa</i> var. <i>sinuosa</i>	Fa	-	-	+	D	h	(15-28)	-	-	-	a
<i>Plagiochila squamulosa</i> var. <i>squamulosa</i>	Fa	+	-	+	D	m,h	(15-28)	-	-	-	a
<i>Plagiochila subalpina</i>	Ma	-	-	-		a	(15-28)	B1,fD	-	B1	h
<i>Plagiochila terebrans</i>	Fa	+	-	+	D	l,m	20-22	fD	-	B1,Be	l,m
Porellaceae											
<i>Porella subdentata</i>	Ma	-	-	+	D	a	(24-80)	-	-	-	a
Radulaceae											
<i>Radula appressa</i>	Ma	-	-	+		a	(15-55)	B1	-	B1	a,l
<i>Radula boryana</i>	Ma	-	-	+	D	a,l	30-35	{B1,Ge}	-	-	a,l
<i>Radula comorensis</i>	Ma	+	-	+	D	a,l	(15-55)	B1	-	B1	a,l
<i>Radula flaccida</i>	Ma	-	-	+		a	15-18	Ge	-	Ge	h
<i>Radula holstiana</i>	Ma	-	-	+	M	a	18-22	-	-	B1,Ge	a,l
<i>Radula javanica</i>	Ma	-	-	+	D	a	(15-55)	B1	-	B1	a,l
<i>Radula quadrata</i>	Ma	-	-	+	D	a	(15-55)	Ge	-	Ge	h
Musci											
Brachytheciaceae											
<i>Brachythecium salebrosum</i>	We	-	-	+	Mat	a	12-18	-	-	-	a
<i>Brachythecium vellerum</i>	We	+	-	+	D	m		-	-	-	e
Bryaceae											
<i>Brachymenium nepalense</i>	sT	+	-	+	D	h	25	-	-	-	a
<i>Brachymenium rigidum</i>	sT	+	-	+	D	h	19-27	-	-	-	a
<i>Brachymenium speirocladum</i>	sT	+	-	+	D	h	15-20	-	-	-	a
<i>Orthodontium gracile</i>	sT	+	-	+	M	h	10-18	-	-	[Ge]	a
Calymperaceae											
<i>Syrrhopodon ermetus</i> ssp. <i>insularum</i>	sT	-	-	+	D	a	(15-35)	-	-	(Ge)	a
<i>Syrrhopodon gardneri</i>	sT	-	-	+	D	l	13-18	Ge	-	(Ge)	m
<i>Syrrhopodon gaudichaudii</i>	sT	-	-	+	D	a	(15-35)	Ge	-	(Ge)	h
<i>Syrrhopodon incompletus</i>	sT	-	-	+	D	a	(15-35)	-	-	(Ge)	a
Dicranaceae											
<i>Bryohumbertia flavicone</i>	sT	+	-	+	D	a,l	14-15	-	-	-	a
<i>Campylopus hildebrandtii</i>	tT	+	-	+	D	h	11-14	-	-	-	a
<i>Campylopus nivelis</i>	tT	+	-	+	D	h	13-16	-	-	-	a
<i>Campylopus perichaetialis</i>	sT	-	-	+	D	a		-	-	Ge	a,l
<i>Dicranum johnstonii</i>	tT	-	-	-	D	a		Ge	-	-	a,l
<i>Leucoloma holstii</i>	We	-	-	+	D	a		-	-	-	a

Entodontaceae												
Entodon adyris	Ma	+	-	+	Mat	h	17-23	-	-	-	a	A _g
Entodon vulcanicus	Ma	+	-	+	D	h	(17-23)	-	-	-	a	A _g
Fissidentaceae												
Fissidens borgenii	sT	+	-	-	D	a, l		-	-	-	a	A _p
Fissidens glauculus	sT	+	-	+	M	m	8-9	-	-	-	a	A _g
Fissidens microcerpus	sT	-	-	-		a		-	-	-	a	A _p
Hookeriaceae												
Callicostella lacerans	Ma	+	-	-	D	h		-	-	-	a	A _g
Daltonia mildbraedii	Ma	+	-	-	D	h	15-17	-	-	-	a	A _g
Lepidopilidium theriotii	sT	-	-	-		a		-	-	-	a	A _p
Lepidopilum lastii	sT	-	-	-		a		-	-	-	a	A _p
Lopidium hemiloma	Fa	-	-	-	D	a		Ge	-	(Ge)	m	A _v
Hypnaceae												
Chrysohypnum frondosum	Ma	-	-	+	Mat	m		-	-	-	a	A _g
Hypnum cupressiforme var. cupressiforme	Ma	-	-	+	D	m	12-18	fD	-	fD	m	F1, A _g
Hypnum cupressiforme var. townsendii	Ma	-	-	+	D	m	12-18	fD	-	fD	m	F1, A _g
Isopterygium mbangae	We	-	-	-	Mat	a		-	-	-	a	A _p
Mittenothamnium reptans	Fa	-	-	-	Mat	a		-	-	-	a	A _p
Rhacopilopsis kilimandscharica	We	+	-	+	D	a, l		-	-	-	a	A _p
Rhacopilopsis transvaaliensis	We	-	-	-		a		[fD]	-	-	a	F1, A _p
Rhacopilopsis trinitensis	Ma	-	-	-		a	(17)	-	-	-	a	A _p
Hypopterygiaceae												
Hypopterygium lericinum	Fa	-	-	-	D	a		-	-	(Ge)	a	Sc, A _p
Hypopterygium mildbraedii	De	-	-	-	D	l		-	-	(Ge)	a	Sc, A _p
Leskeaceae												
Hylocomiopsis cylindricarpa	We	+	-	+	Mat	h	40-50	-	-	-	a	P _g
Leucobryaceae												
Leucobryum cf. acutifolium	sT	-	-	+	D	a	15-17	-	-	-	a	A _p
Octoblepharum albidum	sT	+	-	+	Mat	h	17-20	B1, B5	-	+	h	B _{v, g}
Leucophaneaceae												
Leucophanes angustifolium	sT	-	-	+	D	a	15-20	-	-	Ge	a	A _p
Leucophanes mollerii	sT	-	-	+	D	a	10-15	-	-	Ge	a	A _p
Meteoriaceae												
Floribunderia floribunda	Pe	-	-	-	D	a	15-22	-	-	-	a	A _p
Pilotrichella profusicaulis	Pe	+	-	-	D	a, l		B1	-	-	m	A _v
Neckeraceae												
Calyptothecium hoehneltii	Fa	-	-	+	D	a	16-42	fD, Ge	-	Ge	m	F1, Hs, P _v
Homelioidendron piniforme	Fa	-	-	+	D	a	(12-25)	fD	-	(fD)	m	F1, A _v /P _v
Neckera platyantha	Fa	+	-	+	Mat	m	35-45	fD	-	(fD)	a, l	F1, P _g
Neckera remota	Fa	+	-	+	Mat	m, h	20-33(45)	fD	-	(fD)	l	F1, P _g
Porothamnium stipitatum	Fa	+	-	+	D	l	9-17	fD	-	(fD)	l	F1, A _p
Porotrichum elongatum	Fa	+	-	+	D	l		fD	-	(fD)	l	F1, A _p
Porotrichum molliculum	Fa	+	-	+	D	a	13	fD	-	(fD)	a, l	F1, A _p
Orthotrichaceae												
Macrocoma abyssinica	Ma	+	-	+	D	h	31-56	-	-	(Ge)	a	P _g
Macromitrium bequartii	sT	-	-	-		a		-	-	(Ge)	a	P _p
Schlotheimia cf. bequartii	Cu	-	-	-	M	a		-	-	(Ge)	a	P _p

	Life-form	Sexual diaspores			Monoecious/dioecious	Sexual reproduction	Spores (ø in µm)	Asexual diaspores			Asexual reproduction	Others	Life-strategy
		Relevé	Other samples	Literature				Relevé	Other samples	Literature			
<i>Zygodon intermedius</i>	Cu	+	-	-	D	a,l	15-19	Ge	-	(Ge)	h		A _v
<i>Zygodon roccatii</i>	sT	+	-	-	D	l,h		-	-	(Ge)	a		A _p /P _p
Pottiaceae													
<i>Leptodontium viticulosoides</i>	tT	+	-	+	M,D	h	17-20(25)	-	-	-	a		A _g
Rhizogoniaceae													
<i>Pyrrhobryum spiniforme</i>	tT	+	+	+	M	h	14-16	-	-	-	a		A _g
Sematophyllaceae													
<i>Acroporium prionophylax</i>	Ma	+	-	+	M	a,l	(15)20-22	-	-	-	a		A _p
<i>Donnellia metutina</i>	We	-	-	+	Mat	a		-	-	-	a		A _p
<i>Sematophyllum brachytheciiforme</i>	Ma	+	-	+	M	h	22-28	-	-	-	a		P _g
<i>Sematophyllum nebulosum</i>	Ma	-	-	+		a		-	-	-	a		A _p /P _p
<i>Sematophyllum stylites</i>	Ma	+	-	+	Mat	m	14	-	-	-	a		A _g
<i>Trichosteleum percilleanum</i>	Ma	-	-	-	Mat	e		-	-	-	a		A _p
<i>Wijkia trichocolea</i>	We	-	-	-		a		-	-	-	a		A _p
Thuidiaceae													
<i>Thuidium chenagonii</i>	Ma	-	-	-		a		-	-	-	e		A _p
<i>Thuidium versicolor</i>	We	+	-	-	D	m		-	-	-	a		A _g

Tab. 2. Characters and life strategies of the taxa of the epiphytic bryophyte communities of eastern Zaire (Mt. Biega, Mt. Kahuzi) and Rwanda (Forêt de Nyungwe). [+ present; - absent; [] data uncertain; () character of the genus; empty field: no data available; a absent, not observed; aT adventive shoots/thalli; Bl breaking-off of leaf tips; Bs breaking-off of shoots; Cu cushion; D dioecious; De dendroid; Fa fan; fD flagelliform diaspores (stoloniferous shoots or branches with a gradual attenuation from ordinary leaves at the branch base to vestigial-leaved branch tips); Fl flagellae; Fr fragmentation; Ge gemmae; h high; Hs heterospore; l low, M monoecious; m middle; Ma mat; Mat autoecious; Pe pendant; Sc shoots creeping, rhizome-like; sT short-turf; tT tall-turf; We weft; A_g-P_v life-strategies, cf. Tab. 1.]. For author's names of the taxa cf. Kürschner 1995a.

Tab. 3. (p. 141) Life strategies and mean percentage cover values (%) within the altitudinal gradient of eastern Zaire (Mt. Biega, Mt. Kahuzi) and Rwanda (Forêt de Nyungwe) (for abbreviations see Tab. 1).

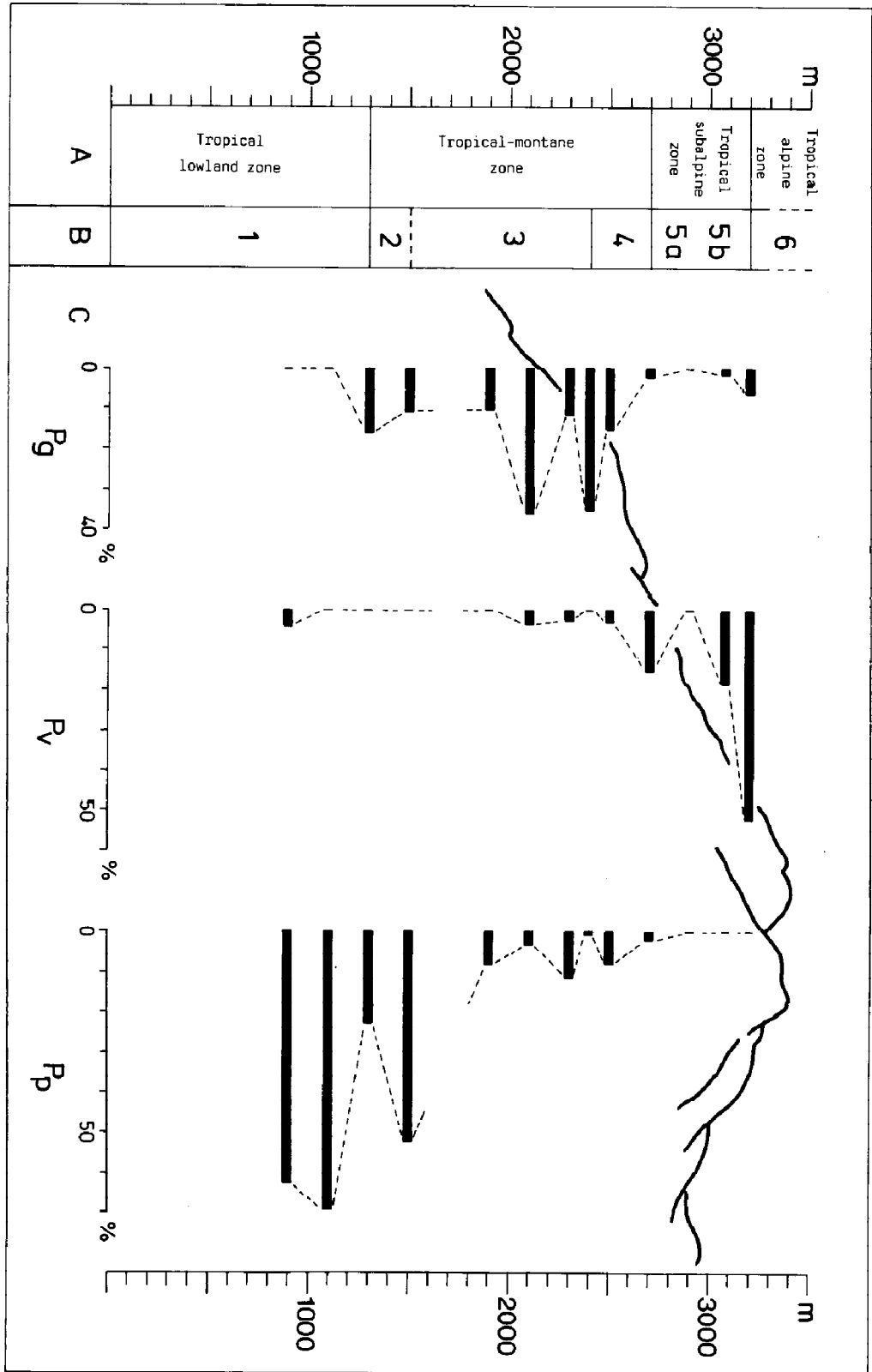
Fig. 2. (p. 142) Life strategies (P_g, P_v, P_p for abbreviations see Tab. 1; mean percentage cover values in %) and their distribution in the altitudinal gradient (200 m-isohypse intervals, C) of eastern Zaire (Mt. Biega, Mt. Kahuzi) and Rwanda (Forêt de Nyungwe) (for A, B see Fig. 1).

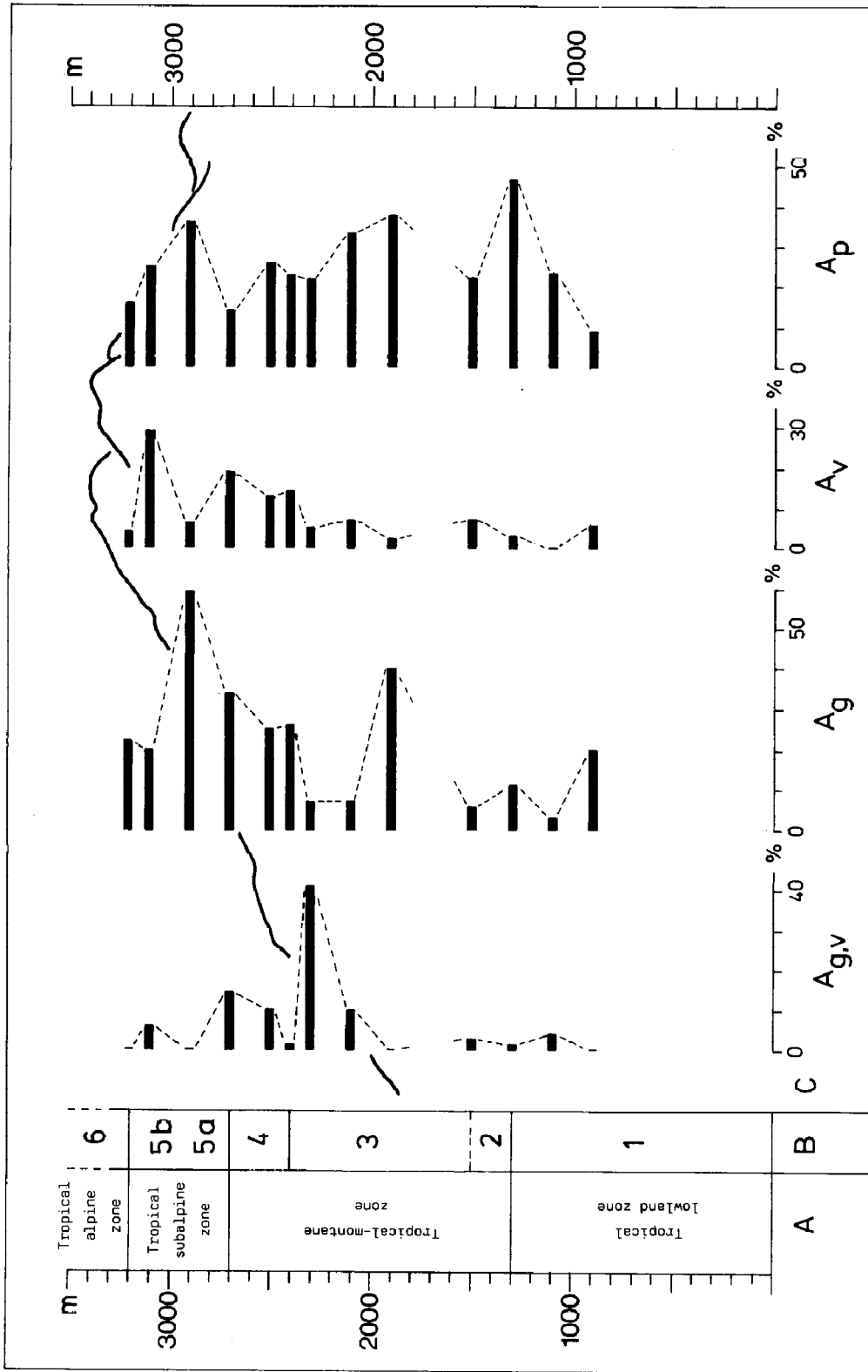
Fig. 3. (p. 143) Life strategies (A_g, A_v, A_p for abbreviations see Tab. 1; mean percentage cover values in %) and their distribution in the altitudinal gradient (200 m-isohypse intervals, C) of eastern Zaire (Mt. Biega, Mt. Kahuzi) and Rwanda (Forêt de Nyungwe) (for A, B see Fig. 1).

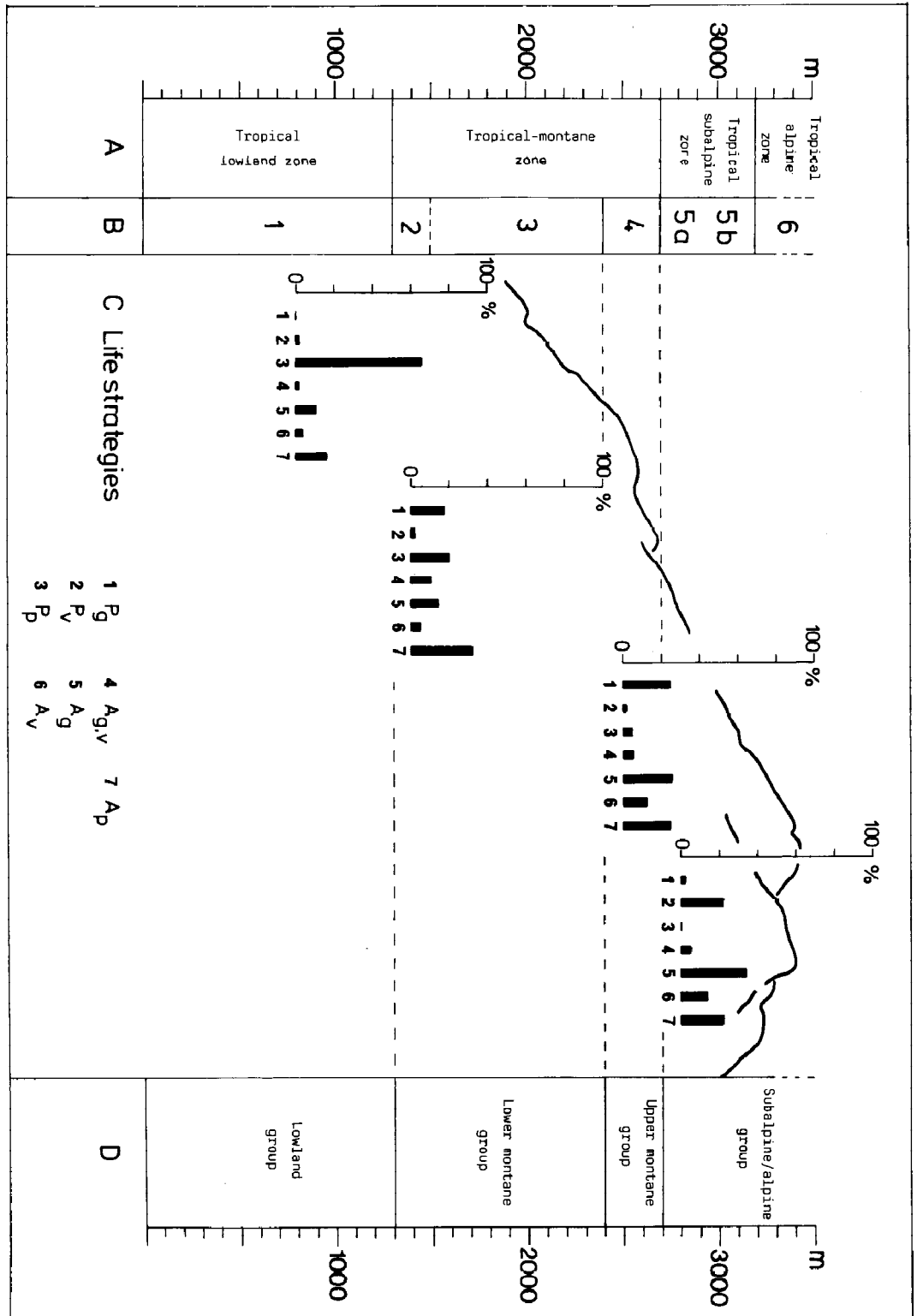
Fig. 4. (p. 144) Life strategies (mean percentage cover values in %) confined to ecological groups (D, cf. Kürschner 1995b) and their distribution in the altitudinal gradient of eastern Zaire (Mt. Biega, Mt. Kahuzi) and Rwanda (Forêt de Nyungwe) (for abbreviations see Tab. 1, for A, B see Fig. 1, for C compare Tab. 3).

Altitude	Ecological group (Kürschner 1995b)										Tropical subalpine/alpine group (4)				Ecological group			
	Lowland group (1)		Lower montane group (2)					Upper montane group (3)			Tropical subalpine/alpine group (4)				(1)	(2)	(3)	(4)
	900	1100	1300	1500	1900	2100	2300	2400	2500	2700	2900	3100	3200-3300	\bar{x}				
No. of species	21	16	21	24	12	30	29	26	56	42	11	18	19					
B _{g,v}	0.2	-	-	-	-	-	-	-	-	-	-	-	-	0.1	-	-	-	
B _g	-	-	-	-	0.7	-	-	-	-	-	-	-	-	-	0.1	-	-	
B _v	-	-	-	-	-	-	0.5	-	-	-	-	-	-	-	-	0.1	-	
P _g	0.2	-	15.2	10.5	10.6	35.9	11.6	37.5	14.9	2.1	-	1.2	6.2	0.1	16.8	25.3	2.4	
P _v	3.3	-	-	-	-	3.4	2.2	-	2.6	15.2	-	18.7	51.9	1.7	1.1	1.3	21.5	
P _p	62.5	69.9	23.1	52.3	8.3	3.3	11.5	0.5	8.6	1.6	-	-	-	66.2	19.7	4.6	0.4	
A _{g,v}	-	3.2	1.1	2.6	-	9.7	41.1	0.2	9.8	14.1	0.2	5.9	-	1.6	10.6	5.0	5.1	
A _g	19.8	3.2	10.3	5.6	40.0	6.9	6.1	26.4	25.6	33.8	57.8	19.6	21.9	11.6	13.8	26.0	33.3	
A _v	5.3	0.2	3.0	7.2	2.2	7.4	4.6	14.2	12.4	19.5	6.0	29.7	3.8	2.7	4.9	13.3	14.8	
A _p	8.7	23.5	47.3	21.8	38.2	33.4	22.3	23.0	26.1	13.7	36.0	24.9	16.2	16.1	32.6	24.6	22.7	

Life strategy







shoots and gemmae and a rather low to nearly absent sexual reproduction (tendency towards reduced sporophyte production) also reach a maximum within the tropical subalpine/alpine zone (Fig. 3), but are confined to wetter sites. This strategy is typical of several liverworts (*Adelanthus decipiens*, *Bazzania roccatii*, *Chiloscyphus muricatus*, *Lepidozia cupressina*, *Radula flaccida*) and *Pilotrichella profusicaulis*, which are dominating the misty upper montane forest (*Podocarpus-Syzygium-Psychotria* community), the ericaceous woodlands and the wet *Podocarpus-Syzygium rowlandii* swamp forest. Nothing is known about the competitive advantage and the potential adaptive value of these asexual diaspores, but the high dominance of these species in the Plagiochilo-Lejeuneetum hepaticolae, the Plagiochilo-Evansiolejeuneetum roccatii and the Pilotrichello-Frullanietum angulatae (Tab. 4, Fig. 5) suppose a high effort of this type in clonal growth and propagation.

Most of the epiphytic species (58 taxa) of the transect belong to the strategy Perennial stayers with moderate or low sexual and asexual reproductive effort (A_p). This strategy is present in all altitudinal zones (Fig. 3), ecological groups (Fig. 4) and communities (Fig. 5), reaching a maximum within the upper tropical lowland zone [Marchesinio-Plagiochiletum salvadoricae prionolejeuneetosum serrulae of the *Julbernardia-Ocotea* transition forest, (Fig. 5)] and the tropical montane zone (Lejeuneo-Plagiochiletum divergentis of the Laurisilvae, Pilotrichello-Frullanietum angulatae of the *Podocarpus-Syzygium rowlandii* swamp forest, Tab. 4, Fig. 5). Beside a long life span, the low reproduction tactic and the small spores, taxa of this strategy are characterized by dioecism (e.g. male and female plants have to be in close proximity for fertilization and sporophyte formation). Most of the Lejeuneaceae (e.g. *Aphanolejeunea exigua*, *Cheilolejeunea pluriplicata*, *Evansiolejeunea roccatii*, *Leucolejeunea xanthocarpa*, *Microlejeunea africana*, *Prionolejeunea serrula*, *Schiffnerolejeunea altimontana*) analyzed, but also *Bazzania decrescens*, *Lepidozia stuhlmannii*, *Metzgeria leptoneura*, *Plagiochila heterostipa*, *Radula holstiana* (liverworts), *Brachythecium vellereum*, *Bryohumbertia flavicoma*, *Leucoloma holstii*, *Leucophanes angustifolium*, *L. molleri*,

the *Rhacopilopsis* species and most of the Sematophyllaceae (mosses) belong to this life strategy. Their dominance and high cover value within the epiphytic communities often results on clonal growth. Within the upper tropical lowland zone and the lower tropical montane zone this strategy fits well in the more or less constant environmental conditions, typical of the Perennial stayer strategy. Summarizing the results, and with regard to the life strategy analysis of the BRYOTROP II-transect (Mt. Kinabalu/Borneo, Frey & Kürschner 1991b), a frequent change of life strategies within epiphytic bryophytes along altitudinal gradients can be observed, and first tendencies concerning the distribution and evolution of life strategies can be outlined. Despite till yet, no example from the South-American hylaea is analyzed, these tendencies seem to be of a more general validity, typical of tropical and non-tropical epiphytic ecosystems.

Perennial shuttle species (P_p) and Perennial stayers (A_p) with moderately or low sexual and asexual reproductive effort, in both tropical ecosystems are confined mainly to the epiphytic communities of the tropical lowland and the lower tropical montane zone. This strategy is typical of epiphytes, especially liverworts (Lejeuneaceae, Frullaniaceae, Radulaceae with a similar basic architecture) of undisturbed primary rain-forest communities, growing under a well balanced, high temperature and humidity regime.

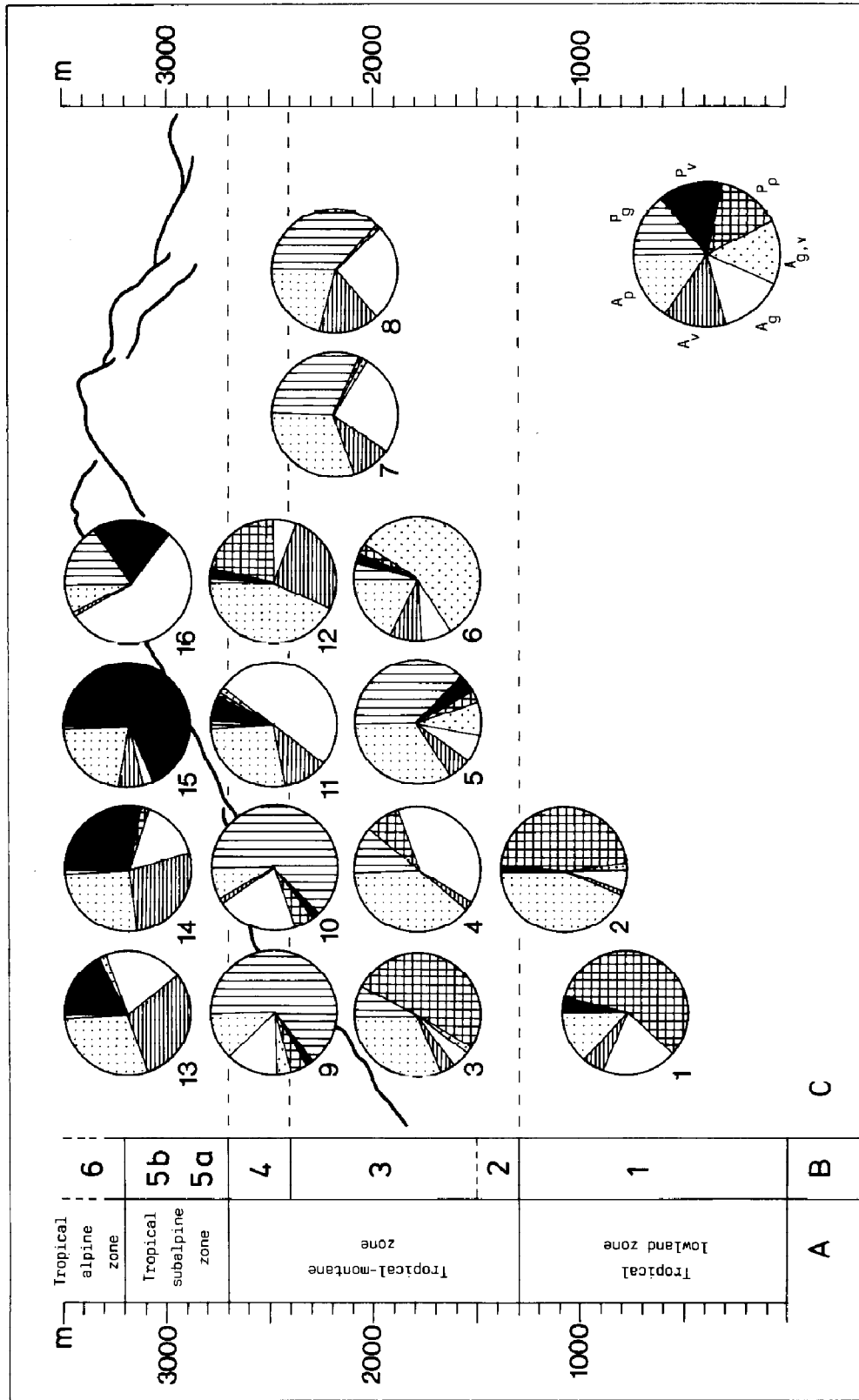
Within the montane rain-forests and the cloudy moss forests of the upper tropical montane zone, the life strategy changes. As in the Mt. Kinabalu transect, in the eastern Congo basin and the adjacent mountains, Perennial shuttle species with high asexual reproductive effort (P_v), e.g. an increased reliance on asexual propagules and clonal growth for population maintenance dominate, and the sporophyte production is much reduced. The characters, typical of this strategy (Tab. 1) must be seen as a set of co-evolved adaptations to the perhumid, cloudy and misty and cooler climate of this distinct altitudinal zone, favouring an asexual reproduction and the growth of epiphytes.

This life strategy is replaced in the secondary woodlands and the unique ericaceous woodlands and the *Dendrosenecio* subpáramo (upper tropical montane and tropical subalpine/alpine zone) of

	Associations (Kürschner 1995a)	Life strategy										
		B _{v,g}	B _g	B _v	P _g	P _v	P _p	A _{g,v}	A _g	A _v	A _p	
Lejeuneo flavae Plagiochilium salvadoricae	1	Marchesinin-Plagiochiletum salvadoricae plagiochiletosum praemorsee	0.1	-	-	3.4	58.3	-	19.9	5.4	12.9	
	2	Marchesinio-Plagiochiletum salvadoricae prionolejeuneetosum serrulae	-	-	-	1.1	46.9	1.7	5.7	0.1	44.5	
Plagiochilium divergentis	3	Lejeuneo-Plagiochiletum divergentis plagiochiletosum fusiferae	-	-	0.2	7.6	-	50.9	1.7	4.8	3.9	30.8
	4	Lejeuneo-Plagiochiletum divergentis plagiochiletosum heterostipae	-	0.7	-	10.5	-	8.2	-	39.5	2.2	38.8
	5	Lejeuneo-Plagiochiletum divergentis typicum	-	-	-	38.1	4.6	2.8	7.4	7.0	5.9	34.2
	6	Plagiochiletum terebrantis	-	-	-	3.9	2.4	2.4	57.8	7.9	8.2	17.4
	7	Drepanolejeuneo-Microlejeuneetum africanae plagiochiletosum divergentis	-	-	-	31.5	-	0.6	1.1	25.8	9.9	31.1
Plagiochilium squamosae	8	Drepanolejeuneo-Microlejeuneetum africanae plagiochiletosum squamosae	-	-	-	36.8	-	0.1	-	26.6	15.4	21.1
	9	Plagiochiletum squamosae	-	-	-	65.3	1.6	4.6	3.6	12.8	-	12.1
	10	Frullanio-Hylocomiopsietum cylindricarpae	-	-	-	62.3	1.8	5.1	-	21.2	1.0	8.6
	11	Orthodontio-Campylopetum hildebrandtii	-	-	-	1.7	6.1	0.3	0.3	52.2	11.6	27.3
12	Pilotrichello-Frullarietum angulatae	-	-	-	0.7	2.8	21.3	-	5.7	26.5	43.0	
Plagiochilium colorantis	13	Plagiochilo-Lejeuneetum hepaticolae	-	-	-	0.9	17.3	-	1.9	19.9	30.1	29.9
	14	Plagiochilo-Evansiolejeuneetum roccatii campylopetosum hildebrandtii	-	-	-	0.5	28.2	1.7	-	15.6	27.6	26.4
	15	Plagiochilo-Evansiolejeuneetum roccatii herbertetosum doggeltiani	-	-	-	0.5	69.2	-	-	2.7	6.1	21.5
	16	Sematophyllo-Campylopetum nivialis	-	-	-	15.9	19.9	-	-	57.0	0.2	7.0

Tab. 4. Life strategies and mean percentage cover values (%) in the epiphytic bryophyte communities of eastern Zaire (Mt. Biega, Mt. Kahuzi) and Rwanda (Forêt de Nyungwe) (for abbreviations see Tab. 1).

Fig. 5. (p. 147) Life strategies (mean percentage cover values in %) within the bryophyte communities of the Lejeuneo flavae-Plagiochilium salvadoricae (1,2), the Plagiochilium divergentis (3-7), the Plagiochilium squamosae (8-12) and the Plagiochilium colorantis (13-16) in eastern Zaire (Mt. Biega, Mt. Kahuzi) and Rwanda (Forêt de Nyungwe) (C). (For the syntaxonomic nomenclature (1-16) and values below 1 % see Tab. 4; for A, B see Fig. 1).



the African volcanos by Perennial shuttle species (P_g) and Perennial stayers (A_g) with high sexual reproductive effort. Under the already xeric conditions, the strong diurnal climatic variations and the heavy winds of the subalpine/alpine zone, numerous mosses typical of the epiphytic communities, are building regularly sporophytes. Their small spores, produced in large numbers, can reach the distant phorophytes, establishing new populations. Taxa with high asexual reproductive effort (e.g. Herbertaceae) in this zone are confined to sites, strongly influenced by the daily mists, rising up from the upper montane zone. Within the woodlands of the upper tropical montane zone, the epiphytes mainly show a shuttle strategy, characterized by relatively large spores. They have a lower dispersal capacity, but probably better chances of successful establishing in the diaspore bank of these woodlands. This indicates, that with increasing aridity, the asexual reproductive effort of tropical, as well as non-tropical epiphytic bryophytes (Frey & Kürschner 1995a) declines.

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References

- Correns, C. 1899:** Untersuchungen über die Vermehrung der Laubmoose durch Brutorgane und Stecklinge. Jena.
- During, H.J. 1979:** Life strategies of bryophytes: a preliminary review. *Lindbergia* 5: 2-18.
- During, H.J. 1981:** Bryophyte flora and vegetation of Lanzarote, Canary Islands. *Lindbergia* 7: 113-125.
- During, H.J. 1992:** Ecological classification of bryophytes and lichens. - In: Bates, J.W. & A.M. Farmer (eds.): *Bryophytes and lichens in a changing environment*, pp. 1-31. Oxford.
- During, H.J. & B. ter Horst 1985:** Life span, mortality and establishment of bryophytes in two contrasting habitats. *Abstracta Botanica* 9, Supplement 2: 145-158.
- Fleischer, M. 1900-1922:** Die Musci der Flora von Buitenzorg. Vols. 1-4. Leiden.
- Frey, W. & H. Kürschner 1991a:** Lebensstrategien von terrestrischen Bryophyten in der Judäischen Wüste. *Botanica Acta* 104: 172-182.
- Frey, W. & H. Kürschner 1991b:** Lebensstrategien epiphytischer Bryophyten im tropischen Tieflands- und Bergregenwald am Mt. Kinabalu (Sabah, Nord-Borneo). *Nova Hedwigia* 53: 307-330.
- Frey, W. & H. Kürschner 1991c:** Das Fossombronio-Gigaspermium mouretii in der Judäischen Wüste. 2. Ökosozioökologie und Lebensstrategien. *Cryptogamic Botany* 2: 73-84.
- Frey, W. & H. Kürschner 1995a:** Soziologie und Lebensstrategien epiphytischer Bryophyten in Israel und Jordanien. *Nova Hedwigia* 61: 211-232.
- Frey, W. & H. Kürschner 1995b:** Bryosoziologische Untersuchungen in Jordanien 3. Lebensstrategienanalyse der terrestrischen und epilithischen Moosgesellschaften. *Fragmenta Floristica et Geobotanica* 40 (im Druck).
- Grime, J.P., E.R. Rincon & B.E. Wickerson 1990:** Bryophytes and plant strategy theory. *Botanical Journal of the Linnean Society* 104: 175-186.
- Hedberg, O. 1951:** Vegetation belts of the East African mountains. *Svensk Botanisk Tidskrift* 45: 140-202.
- Klötzli, F. 1958:** Zur Pflanzensoziologie des Südhanges der alpinen Stufe des Kilimandscharo. *Berichte des Geobotanischen Forschungsinstituts Rübel in Zürich* 1957: 33-59.
- Kürschner, H. 1994:** Adaptionen und Lebensstrategien in basiphytischen Gesteinsmoosgesellschaften am Nordrand der Schwäbischen Alb (Süddeutschland). *Phytocoenologia* 24: 531-558.
- Kürschner, H. 1995a:** Epiphytische Moosgesellschaften im östlichen Kongobecken und den angrenzenden Gebirgsstöcken (Parc National de Kahuzi-Biega/Zaire, Forêt de Nyungwe/Rwanda). *Wissenschaftliche Ergebnisse der BRYOTROP-Expedition nach Zaire und Rwanda* Nr. 4. *Nova Hedwigia* 61: 1-64.
- Kürschner, H. 1995b:** Höhengliederung epiphytischer Moose im östlichen Kongobecken und den angrenzenden Gebirgsstöcken (Parc National

de Kahuzi-Biega/Zaire, Forêt de Nyungwe/Rwanda). Wissenschaftliche Ergebnisse der BRYOTROP-Expedition nach Zaire und Rwanda Nr. 5. Tropical Bryology 11:77-85.

Miles, C.J. & R.E. Longton 1992: Spore structure and reproductive biology in *Archidium alternifolium* (Dicks. ex Hedw.) Schimp. Journal of Bryology 17: 203-222.

Prioul, C. & P. Sirven 1981: Atlas du Rwanda, 23 tabl. Kigali, Paris, Nantes.

Schuster, R.M. 1988: Ecology, reproduction biology and dispersal of Hepaticae in the Tropics. Journal of the Hattori Botanical Laboratory 64: 237-269.

Stearns, S.C. 1976: Life history tactics: a review of the ideas. Quarterly Review of Biology 51: 3-47.

Stoneburner, A., D.M. Lane & L.E. Anderson 1992: Spore dispersal distances in *Atrichum angustatum* (Polytrichaceae). The Bryologist 95: 324-328.

