SALTATORIA COENOSES OF HIGH-ALTITUDE GRASSLANDS ON MT. KILIMANJARO, TANZANIA (ORTHOPTERA: SALTATORIA)

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Abstract. From 1996 to 2001 field studies on Saltatoria were undertaken in half-year periods from October to April and August to September on the southern slopes of Mt. Kilimanjaro, Tanzania. The focus was on the high-altitude grasslands of the lower montane (1600–1900 m) and subalpine zone (2700–3200 m). Based on phytosociological relevés applying the method of Braun-Blanquet (1964), the grasshopper composition of 52 plots was recorded. Three grasshopper coenoses in three plant communities could be distinguished. Using knowledge of the habitat preferences of Saltatoria the distribution pattern of locally restricted species can be understood, which is here shown for flightless species on the southern slopes of Mt. Kilimanjaro. Accepted 17 January 2003.

Key words: Saltatoria, grasshopper coenoses, montane and subalpine tropical grasslands, plant sociology, speciation, bioindication, Mt. Kilimanjaro, Tanzania.

INTRODUCTION

Mt. Kilimanjaro has a variety of ecological zones due to its enormous altitudinal range of about 5000 m and a precipitation that differs with altitude and exposition of the mountain massif. Ecological zones are represented by wet and arid savanna habitats (800–1000 m), dry to moist grasslands as well as shady banana plantations in the cultivation belt (1000–1600 m), clearings and differently disturbed and undisturbed forests in the montane zone (1600–ca. 3000 m), and (sub)alpine grass- and heathlands (2700–4500 m). Accordingly a great variety of grasshopper species is found, ranging from typical widely distributed savanna species to endemic species only occurring in forest communities or originating from them.

A general inventory of the fauna of Mt. Kilimanjaro, including Saltatoria, was undertaken by an expedition led by Sjöstedt in the beginning of the last century (Sjöstedt 1909). Most papers on African Acridoidea are of a taxonomical nature (e.g., Bolivar 1930, Dirsh 1965, Descamps 1977), some including keys to the species (e.g., Dirsh 1955; Jago 1966, 1981, 1994; Hollis 1968, 1971; Kevan 1970; Ritchie 1982; Grunshaw 1986) or lists of single areas (e.g., John-

Grasshoppers are an effective group for bioindication because of their sharp reaction to climatic factors. With the aid of indicator species it is possible to measure the quality of certain habitats. In Central European habitats various studies have already proved the usefulness of Saltatoria for measuring the quality of grasslands (e.g., Marchant 1953; Schmidt & Schlimm 1984; Federschmidt 1989; Reich 1991; Detzel 1992, 1998; Hemp & Hemp 1996, 2000; Ingrisch & Köhler 1998).

In the present study, supported by the phytosociological method of Braun-Blanquet (1964), Saltatoria coenoses are described for grasslands between 1600 and 1900 m and 2700 to 3200 m on the southern slopes of Mt. Kilimanjaro. Analogous to a plant sociological evaluation, the Saltatoria relevés were united in a table making coenoses apparent and dependent on certain plant communities. Detailed habitat requirements for Saltatoria species can be derived and information for bioindication obtained

ston 1937; Kevan 1954, 1967). Comparatively few studies deal with the ecology of African grasshoppers (e.g., Joyce 1952, Robertson & Chapman 1962, Vesey-Fitzgerald 1964, Phipps 1966, Hochkirch 1996). Especially African Ensifera are very poorly investigated, with few keys published for groups like Saginae (Kaltenbach 1972), Phaneropterinae (e.g., Ragge 1980), or just single genera (e.g., Bailey 1975).

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to measure the degree of disturbance of habitats. Processes of distributional patterns and modes of speciation can be explained.

RESEARCH AREA

Mt. Kilimanjaro is located 300 km south of the equator in Tanzania on the border to Kenya between 2°45' and 3°25'S and 37°00' and 37°43'E. This study was carried out on the southern slopes of Mt. Kilimanjaro in Tanzania (Fig. 1).

Mt. Kilimanjaro is a more or less eroded relict of an ancient volcano with three peaks of different ages rising from the savanna plains at 700 m a.s.l. to a snow-clad summit of 5895 m. The Shira is the oldest part and forms today a wide plateau. The 5125 m high Mawenzi is also a volcano ruin. Only the main peak, Kibo, shows the typical cone shape of a volcano.

The foothills of the southern slopes receive an annual rainfall of 800–900 mm and the lower slopes at 1500 m receive 1500–2000 mm. The forest belt between 2000 and 2300 m receives in places over 3000 mm (Hemp, A. 2002), which is more than on other high mountains of East Africa. In the alpine zone the precipitation decreases to 200 mm. The northern slopes have much lower annual rainfall, being in the rain shadow caused by the peaks themselves. The rainfall is seasonal, the two rainy seasons being from March to June and from November to December.

According to the changing climatic conditions several vegetation zones are apparent on the southern slopes of Mt. Kilimanjaro (Table 1). Between 700 and 1000 m a.s.l. the dry and hot savanna zone stretches around the mountain base, where most areas are farmed with maize, beans and sunflowers, in West Kilimanjaro with wheat. Around Lake Chala at the eastern foot of the mountain, and around Ngare Nairobi of West Kilimanjaro, savanna grasslands are still intact, providing important habitats for Saltatoria and other invertebrates. However, larger mammals are almost extinct in these areas nowadays.

The main cultivation zone is located between 1000 and 1800 m. This area is intensively cultivated by the Bantu tribe of the Wachagga using an agroforestry system. Most of the former evergreen forest has been replaced by banana-coffee plantations. Some species of the tree layer still exist in the banana-coffee plantations, serving as shade trees and used for fire-

wood, such as *Albizia shimperiana*, *Olea capensis* or *Ekebergia capensis* (Hemp, A. 1999, Hemp *et al.* 1999).

In the cultivated submontane zone of the southern slopes of Mt. Kilimanjaro, forest remnants are restricted to deep valleys and gorges with small relicts of *Leptonychia usambarensis* gorge forests and *Mitragyna rubrostipulata* riverine forests. This forest type very much resembles the very diverse wet submontane (intermediate) forests of the Pare and Usambara Mts. and is floristically completely different from the montane forests at higher altitudes on Mt. Kilimanjaro (Hemp, A. 2001). Nearly all of these submontane gorge forests with their unique flora are today completely destroyed by human influence.

The montane forest belt girdles the whole mountain. On the southern slopes of Mt. Kilimanjaro the so-called half-mile forest strip stretches between 1600 and 1900 m, bordering the natural forest. This area is meant for timber production, but in most places is heavily over-used and in certain areas covered by meadow communities.

The most important tree species in the montane forests of the wet southern slopes is the camphor tree (Ocotea usambarensis). In the lower montane zone (1600–2100 m) Ocotea usambarensis is associated with Agauria salicifolia, Macaranga kilimanjarica, and Polyscias fulva. This forest zone is heavily influenced by human impact, as can be seen from the forest composition: Agauria, an Ericaceae, is favored by (manmade) fires, and the two latter species are trees which dominate the forests after the logging of camphor (cf. Lambrechts et al. 2002).

The middle montane zone (2100–2400 m) is the main habitat of the camphor tree (Ocotea usambarensis), where it builts pure stands. A characteristic constituent of the montane forests on the southern slope is the tree fern Cyathea manniana, indicating the high humidity of this part of the mountain. This tree fern plays an important role in forest regeneration. In gorges and along streams Afrocrania volkensii is a typical feature of the tree layer. In the upper montane zone (2400-2800 m) the gymnosperm Podocarpus latifolius starts to prevail. The lower subalpine zone (2800-3100 m) is dominated by Podocarpus latifolius, Hagenia abyssinica, and Prunus africana. At this altitude Erica excelsa also plays an important role in the forests, replacing *Podocarpus* after fire (Hemp & Beck, 2001). Erica excelsa stands form the upper forest border in the middle subalpine zone (3100–3600 m).



TABLE 1. Altitudinal zones and main vegetation units on Mt. Kilimanjaro.

m asl	Main vegetation type		nal zone acc emp, A. (20		m asl
4400 4300 4200 4100 4000 3900	Helichrysum cushion vegetation	11	lower	alpine	4400 4300 4200 4100 4000 3900
3800 3700 3600	Erica shrubland, Helichrysum cushion vegetation	10	upper		3800 3700 3600
3500 3400 3300 3200 3100	Erica shrubland, Erica excelsa forest, Hagenia-Rapanea forest	9	middle	subalpine	3500 3400 3300 3200 3100
3000 2900 2800	Erica excelsa forest, Podocarpus forest, moorland	8	lower		3000 2900 2800
2700 2600 2500 2400	Podocarpus-Ocotea forest, Erica excelsa forest	7	пррет		2700 2600 2500 2400
2300 2200 2100	Ocotea-Podocarpus forest	6	middl.	nontane	2300 2200 2100
2000 1900 1800	Agauria-Ocotea forest, Cassipourea forest	5	lower] E	2000 1900 1800
1700 1600	Agauria-Ocotea forest, coffee-banana plantations, Bulbostylis meadows	4	Ť		$-\frac{1700}{1600}$
1500 1400 1300	coffee-banana plantations, Croton-Olea forest, Hyparrhenia meadows	3	upper	ıtane	1500 1400 1300
1200 1100 1000 900	coffee-banana plantations, savanna bushland and grassland, agriculture, pasture	2	lower	submontane	1200 1100 1000 900
800 700	savanna bushland and grassland, agriculture, pasture	1		col- line	800 700

The *Erica excelsa* forests are gradually replaced by *Erica* bush between 3100 and 3500 m a.s.l. In the south-eastern parts moorlands dominated by tussock grass fringe the forest, due to regular fires in this zone (Hemp & Beck, 2001). At an altitude of about 3900 m the *Erica* heathlands grade into *Helichrysum* cushion vegetation that reaches up to 4500 m. Higher altitudes are very poor in vegetation while the highest

elevations of Kibo peak are covered with glaciers (see aspects of the (sub) alpine vegetation of Mt. Kilimanjaro in Hedberg 1951, Klötzli 1958, Beck *et al.* 1983). A constancy table of the different vegetations units of forests and open habitats on Mt. Kilimanjaro is given by Hemp, A. (2001).

Investigated habitats. This paper concentrates on the Saltatoria coenoses of the high-altitude grasslands (Fig.

1) on the lower forest border in the montane zone and above the upper forest border in the subalpine zone. The grasshopper composition of grasslands at lower altitudes and of forests is in preparation.

METHODS

Vegetation and orthopterological field work was carried out parallel in the years 1996 to 2001. Many plots were investigated at intervals of 2–3 months during the field study periods October-April and August-September, and some remote plots were checked 2–3 times at different times or years. Thus the relevés were complemented with species not recorded in earlier visits to the plots.

Using the Braun-Blanquet (1964) method, 70 vegetation relevés were made in montane and subalpine grasslands. Special attention was given to homogeneity. The relevé size was chosen with respect to the minimum area and was mostly 100 m² in subalpine grasslands and 25 m² in montane grasslands.

The relevés were clustered according to floristic similarity and the resulting plant communities are presented in Table 4 using the Braun-Blanquet scale with the following symbols: 5 = 75-100% cover, 4 = 50-75%, 3 = 25-50%, 2 = 5-25%, 1 = many individuals with 1-5% cover, + = some individuals with less than 1% cover, + = 1 single individual with very small cover. In Table 4 species with low constancy were omitted. The entire species list may be requested from the authors.

The differentiation of the vegetation units presented in this study from the other plant communities on Mt. Kilimanjaro is based on over 1100 relevés. For demarcation of character and differential species, compare the constancy tables of all vegetation types as given by Hemp, A. (2001). In the headlines of the vegetation table information on the plots such as locality, altitude, inclination, exposition, vegetation cover, and height are given, as well as the number of the grasshopper plot and grasshopper coenosis. Thus, a direct comparison between vegetation and respective grasshopper fauna is possible and the association of a vegetation plot with a distinct grasshopper coenosis is apparent. The floristic nomenclature follows Hubbard et al. (1952), Haines & Lye (1983), Agnew & Agnew (1994), and Beentje (1994).

Parallel to the relevés of a given homogeneous grassland area, Saltatoria species were recorded and their abundance estimated. Analogous to a plant sociological table, the plots were clustered according to their faunistic similarity and the resulting Saltatoria coenoses are presented in Table 5, giving the abundance of grasshopper species as follows: 3 = > 5 specimens/ m^2 , 2 = ca. 5 specimens/ m^2 , 1 = ca. 1 specimen/ m^2 , + = only single specimens in the investigated plot noted, r = one specimen noted in the investigated plot. In this table in addition to the plot numbers the altitude and the species number per relevé are given as well as the number of the vegetation plot. Therefore habitat parameters such as vegetation cover or inclination can be seen in the vegetation table (Table 4) for every grasshopper plot.

The differentiation of the coenoses presented in Table 5 from the other grasshopper coenoses on Mt. Kilimanjaro, and the altitudinal distribution of grasshoppers as given in Table 2 and 3 are based on the evaluation of over 400 plots from savanna to afroalpine grasslands.

RESULTS AND DISCUSSION

Species of the submontane to the afroalpine zones of Mt. Kilimanjaro. Onehundredsix Saltatoria species are said in the literature to occur on Mt. Kilimanjaro, of which 19 were not found during the study period. Additionally, 85 species not yet recorded were collected, mainly on the western, southern, and eastern slopes, resulting in a total number of 191 Saltatoria species for Mt. Kilimanjaro. Sixty-six species were noted in the submontane, montane, and subalpine zones on the southern and western slopes of Mt. Kilimanjaro (Table 2).

Eleven Saltatoria species (without Gryllacrididae) are endemic to Mt. Kilimanjaro, and all except for the thericleid Lophothericles kongoni Sjöstedt, 1909 are representatives of the submontane-montane zone (Table 3). These species must be regarded as being adapted to mountainous habitats. The total number of Saltatoria species with their main distribution in the submontane to Afroalpine zone on Mt. Kilimanjaro is over 40 (species with main distribution in the savanna are not considered). In an area completely covered by forest, as could have been the case before human settlement, savanna species were absent from the submontane and montane zone. That the southern slopes of Mt. Kilimanjaro were covered by dense forest even in historical times is reported by Stahl (1964), as trade caravans preferred to climb Mt. Kilimanjaro on the eastern side to pass at the border between montane forest and heathlands rather than finding their way through the dense and dangerous forests of the

TABLE 2. Grasshopper species of the submontane to subalpine zones of Mt. Kilimanjaro with main habitat and altitudinal distribution (altitude of main occurrence underlined) on the southern slopes of Mt. Kilimanjaro. Ab: abundance on the southern slope of Mt. Kilimanjaro as recorded in the years 1996–2001; r: rare (1–5 records), known from few localities: + (5–10 records), common: ++ (10–50 records), abundant: +++ (> 50 records).

Species	Habitat	Altitudinal distribution	AB
Caelifera Tetrigidae			
Leptacrydium gratiosum (Karsch, 1893)	Bulbostylis meadows, Tolpis meadows, swamps of the submontane and montane zones	1400- <u>1600-1800</u>	++
Paratettix histricus (Stål, 1861)	submontane and montane swamps, <i>Bulbostylis</i> meadows, <i>Tolpis</i> meadows, along rivers and irrigation canals, submontane grasslands	900-1800-?	++
Paratettix villiersi Günther, 1979	swamps, <i>Bulbostylis</i> meadows, <i>Tolpis</i> meadows, along irrigation canals of the submontane zone	1600-1700	+
Eumastacidae/ Thericleinae			
Chromothericles kanga (Sjöstedt, 1923)	forest edges and clearings of the submontane and montane forest, often on <i>Rubus steudneri</i>	1500- <u>1700-1800</u> -2700	++
Pyrgomorphidae			
Chrotogonus hemipterus Schaum, 1853	geophilous species, on degraded places with sparse vegetation from the savanna to the lower boundary of the montane forest	<u>800-900-1000</u> -1700	++
Dictyophorus griseus griseus (Reiche & Fairemaire, 1847)	on disturbed ground with open herb vegetation, pest of cultivated fields in the plantation belt	1000- <u>1200-1400</u> -1600	++
Parasphena meruensis meruensis Sjöstedt, 1909	Bulbostylis meadows	1400- <u>1500-1700-</u> 1900	++
Parasphena pulchripes (Gerstaecker, 1869)	subalpine moorland and heathland zone	2700-3000- 4500	++
Phymateus viridipes viridipes Stål, 1873	on herbs and bushes at shady localities of the plantation belt and in much disturbed sub- montane forest to the lower boundary of the montane forest	1200- <u>1400-1600-</u> 1800	++
Phyteumas purpurascens purpurascens (Karsch, 1896)	on herbs and bushes at shady localities of the plantation belt and in much disturbed submontane forest	?-1600-1750	++
Taphronota calliparea immaculata Sjöstedt, 1929	bushes in the plantation belt	1600	r
Zonocerus elegans elegans (Thunberg, 1815) Lentulidae	on grasslands from the savanna to the <i>Bulbostylis</i> meadows; pest of cultivated fields	<u>800-1000</u> -1800	++
Altiusambilla modicicrus	in lush vegetation in shady banana-coffee-	1300- <u>1700-2200</u> -2800	
(Karsch, 1896)	plantations, on moist high-altitude grasslands, forest edges, clearings, montane forest paths	1300- <u>1700-2200</u> -2800	+++
Acrididae Oxyinae			
Oxya hyla hyla Serville, 1831	wet and moist meadow habitats like swamps, rice fields, along canals, water edges, especially in the savanna	<u>800-1000</u> -1400	++
Coptacridinae			
Eucoptacra gowdeyi Uvarov, 1923 Parepistaurus deses deses	Bulbostylis meadows on lush herbs along montane forest roads, sub-	1450- <u>1600-1700</u> -1800 1350- <u>1500-1700-</u> 2000	++
(Karsch, 1896) Parepistaurus lindneri Kevan, 1955	montane forests, shady banana-coffee plantations submontane forest	1300	r

Species	Habitat	Altitudinal distribution	AB
Calliptaminae			
Acorypha laticosta (Karsch, 1896)	submontane grasslands, Bulbostylis meadows	1300-1800	++
Eyprepocnemidinae			
Cataloipus oberthüri oberthüri	dispersal after mature insect appears, larval	<u>800-1000</u> -1800	++
(Bolivar I., 1890) Taramassus cunctator sjöstedti	development in the savanna on open ground in grasslands sparse in	900 1000 1400	
(Ramme, 1929) Taramassus cunctator flabellatus	vegetation, cultivated fields	900- <u>1000</u> -1400	++
(Ramme, 1931)			
Catantopinae			
Abisares viridipennis viridipennis (Burmeister, 1838)	on bushes in the plantation belt, nymphs in humid shady grasslands of submontane zone, in colline forest	900-1500	++
Catantops momboensis momboensis Sjöstedt, 1931	dispersal after mature insect appears, larval development in the savanna	<u>800-1000</u> -1400	++
Diabolocatantops axillaris axillaris (Burmeister, 1838)	dispersal after mature insect appears, larval development in the savanna	<u>800-1000</u> -1400	+
Eupropacris vana (Karsch, 1896)	plantation belt, indigenous <i>Croton-Olea</i> africana forest	1300-1500	+
Hadrolecocatantops kilimandjaricus (Ramme, 1929)	Bulbostylis meadows	<u>1500-1700</u> -1900	+++
Ixalidium sjöstedti Kevan, 1950	at shady places in litter in the plantation belt, Bulbostylis meadows, submontane forest	1350- <u>1400-1600</u> -1900	+++
Phaeocatantops decoratus decoratus (Gerstacker, 1869)	dispersal after mature insect appears, larval development in the savanna	<u>800-1000</u> -1700	++
Cyrtacanthacridinae			
Cyrtacanthacris tatarica tatarica (Linné, 1758)	dispersal after mature insect appears, larval development in the savanna	<u>800-1000</u> -3500	+++
Acanthacris ruficornis ruficornis (Fabricius, 1787)	adults on bushes of degraded submontane forest, nymphs in <i>Bulbostylis</i> and <i>Tolpis</i> meadows	1300- <u>1600-1800-</u> 1900	++
Oedipodinae			
Ailopus longicornis Sjöstedt, 1909	in herb vegetation of roadsides in the submontane zone	1000-1600	++
Ailopus thalassinus (Fabricius, 1781)	wet and moist habitats, in humid herb vegetation of roadsides in the submontane zone	<u>800-1000</u> -1700	++
Gastrimargus africanus africanus (Saussure, 1888)	submontane grasslands, replaced by <i>G. verticalis</i> at about 1200-1300 m, dispersal to higher altitudes after mature insect appears	800- <u>1000-1200</u> -1800	++
Gastrimargus determinatus vitripennis (Saussure, 1888)	dispersal after mature insect appears, larval development in the savanna	<u>800-1000</u> -1700	++
Gastrimargus verticalis verticalis (Saussure, 1884)	submontane grasslands, <i>Bulbostylis</i> meadows	1300- <u>1400-1800</u>	+++
Heteropternis couloniana (Saussure, 1884)	<u>1400-1700</u> -3200	+++	
Morphacris fasciata	Afroalpine zone geophilous species, bare ground from the	800-900, 1300-1800	+++
(Thunberg, 1815) Oedaleus senegalensis (Krauss, 1877)	savanna to border of montane forest dispersal after mature insect appears, larval development in the savanna	<u>800-1000</u> -1700	+++
Acridinae	-		
Acrida sulphuripennis (Gerstäcker, 1869)	dispersal after mature insect appears, larval development in the savanna	-1500	+++

Species	Habitat	Altitudinal distribution	AB
Coryphosima centralis Rehn, 1914	Bulbostylis and Tolpis meadows, moorlands and heathlands	?- <u>1700-1900</u> -3300	+++
Coryphosima stenoptera stenoptera (Schaum, 1853)	open habitats in the plantation belt, submontane grasslands	1200-1400-?	+++
Duronia chloronota (Stål, 1876)	rarely in grasslands of the plantation belt, development in savanna habitats	-1700	++
Gymnobothroides levipes (Karsch, 1896)	Bulbostylis and Tolpis meadows	<u>1600-1700</u> -1900	++
Gymnobothrus temporalis temporalis (Stål, 1876)	submontane grasslands sparse in vegetation, along roadsides, open ground in banana-coffee- plantations	800- <u>1000-1500</u> -1800	+++
Odontomelus brachypterus (Gerstäcker, 1869)	in semi-shade in submontane grasslands, roadside vegetation	<u>1200-1500</u> -1600	++
Truxalis conspurcata somalia Burr, 1902	open paths and grasslands sparse in vegetation in the plantation belt	-1500	+
Uganda kilimandjarica (Sjöstedt, 1909)	moorlands, heathlands	<u>2700-3200</u> -?	++
Ensifera Tettigoniidae Conocephalinae			
Anthracites kilimandjaricus Sjöstedt, 1909	canopy dweller in submontane and montane forest	1600-1800-?	++
Anthracites montium Sjöstedt, 1909 Conocephalus maculatus (Le Guillou, 1841)	canopy dweller in submontane and montane forest savanna grasslands, submontane grasslands	1600-2200-? 900- <u>1000-1300</u> -1600	++ +++
Conocephalus conocephalus (Linné, 1767)	dispersal after mature insect appears, larval development in the savanna	<u>800-1000</u> -1500	+++
Conocephalus kilimandjaricus (Sjöstedt, 1909)	Tolpis meadows, Bulbostylis meadows, lush vegetation on open humid places	1300- <u>1400-1700-</u> 1900-?	+++
Conocephalus kibonotense (Sjöstedt, 1909)	humid places in the plantation belt, high-altitude grasslands, forest edges	1400- <u>1800-2200</u> -?	++
Ruspolia differens (Serville, 1839)	submontane grasslands, dispersal after mature insect appears into all suitable meadow types at the southern slopes	800- <u>1000-1400</u> -1700	++
Ruspolia sp.	Bulbostylis meadows	1400-1800	+
Listroscelidinae			
Aerotegmina kilimandjarica Hemp, 2001	canopy dweller of disturbed and undisturbed submontane and montane forest	<u>1600-2000</u> -2500	++
Meconematinae			
Amytta olindo Hemp, 2001	Bulbostylis meadows, forest edges, humid places in the plantation belt	<u>1400-1600</u> -1900	++
Amytta kilimandjarica Hemp, 2001	disturbed and undisturbed submontane and montane forest	1600-2100	++
Phaneropterinae			
Arantia fasciata (Walker, 1869) Eurycorypha sp.	canopy dweller in the plantation belt montane forest edge of half-mile forest strip, on bushes	?-1400-? ?-1700-?	+
Eurycorypha varia Brunner v. Wattenwyl, 1891	canopy dweller in the plantation belt	?-1400-?	+
Horatosphaga heteromorpha Karsch, 1888	in all meadow types on the southern slopes from the savanna to the lower boundary of the montane forest	800-1800	+++

Species	Habitat	Altitudinal distribution	AB
Horatosphaga montivaga (Sjöstedt, 1909)	clearings of indigenous submontane <i>Olea africana</i> forest at West Kilimanjaro	1500-?	+
Melidia kenyensis Chopard, 1954	canopy dweller in the plantation belt	1300-2000-?	++
Monticolaria kilimandjarica Sjöstedt, 1909	disturbed submontane forest, disturbed and undisturbed montane forest	<u>1600-2200</u> -?	++
Phaneroptera sparsa Stål, 1857	all meadow types of the southern slopes, on open bush vegetation, in bushy vegetation along roads, from the savanna to the lower boundary of the montane forest	800-1800	+++
Plangia sp.	canopy dweller in the plantation belt	?-1400-?	r

slopes and bottom that covered the area continuously between Kilimanjaro and the Lelatema Mts. Today small relicts are seen in the Rau forest which is protected as a water reservoir for Moshi town. Also Volkens (1897) and Engler (1925) described closed evergreen forest communities on the southern slopes of Mt. Kilimanjaro that are now completely lost. Today, with many degraded patches with sparse or no vegetation in the colline to the montane zones, many savanna species find adequate habitats for reproduction. Twenty Saltatoria species are present-day indicators of the dramatic change in the landscape of the southern slopes of Mt. Kilimanjaro. Thus a "savanna effect" of about 30%, that is a change from forest to savanna-like habitats, can be assumed.

Some of the submontane forest species have adapted to a changed environment. When the Chagga people gradually changed the forest into agricultural fields, mainly replacing the bush and herb layers by

field crops, some of the resident Saltatoria coped with this change and found habitats in the Chagga home gardens (e.g., *Ixalidium sjöstedti*, *Altiusambilla modicicrus*, *Parepistaurus deses*) while others disappeared (*Horatosphaga montivaga*, *Parepistaurus lindneri*).

Altiusambilla modicicrus (Fig. 2), Parepistaurus deses, and Ixalidium sjöstedti are found today at altitudes of around 1400 m up to the lower border of the montane forest. On the western side of Mt. Kilimanjaro, where indigenous forest is still present, these species occupy their original habitat (1300–1600 m). In the colline and submontane zones of the southern and eastern slopes nearly every patch of forest has been destroyed.

The actual habitats occupied by the catantopine *Ixalidium sjöstedti* (Fig. 3) suggest that this species has evolved in colline and submontane forest. In the *Olea africana* forests of the western slopes around Sanja Juu at 1300 to 1500 m, and in the relicts of submontane



FIG. 2. The tiny lentulid *Altiusambilla modicicrus* inhabits lush edge vegetation from the submontane to the montane zones.



FIG. 3. *Ixalidium sjöstedti* is well camouflaged among litter of trees. In the montane zone it also occurs on high-altitude meadows.

gorge forests on the southern slopes, it is found on the floor of not too dense forest, while elsewhere it only occurs in semi-shade, e.g., under the canopy of single shade trees higher up in the plantation belt. It probably migrated along edges into higher altitudes and today inhabits even the disturbed lower forest border at 1600-1800 m and also montane grasslands. A similar process in stenoecious species moving to higher altitudes because of the destruction of their habitat can be seen in two Ixalidium species in the East Usambara Mts. I. haematoscelis is reported mainly from lower altitudes in lowland forests (Ramme 1929, Kevan 1950), while I. transiens occurs at higher altitudes in submontane forests with lower temperatures (Hochkirch 1995, 1996). Following the clearing of huge areas in the East Usambara Mts. from the beginning of the last century, I. haematoscelis found adequate living conditions in the now open and thus warmer submontane forests, e.g., along the edges of the tea plantations. In the disturbed forest of the Kwamkoro forest reserve of Amani both species nowadays occur syntopically.

Altiusambilla modicicrus on the other hand is frequently found in banana-coffee plantations, especially where shade trees are left, in the lush vegetation of irrigation canals and shady grasslands at the bottom of small valleys. Possibly this species has found adequate living conditions in the shady plantations and is not as stenoecious as for example H. montivaga. The same can be said for the submontane forests species Parepistaurus deses, which today also occurs in the plantation belt.

P. lindneri was only twice obtained during five half-year collecting field trips, although transects from the savanna to the subalpine zone in 100 m steps were laid and specimens collected. The original description of P. lindneri was from localities at about 1400 m (Kevan 1955). Many changes, that is clearing of forest, have taken place since the 1950s, which might be a reason for the disappearance of this grasshopper species from its type locality. One population of this probably nowadays endangered species on Mt. Kilimanjaro was encountered in a small remnant of submontane forest at 1300 m. This forest, on a small

TABLE 3. Main distribution of Saltatoria species on the southern slopes of Mt. Kilimanjaro; end: endemics; fl: flightless species, in brackets: species which often develop macropterous individuals.

Main habitat	end	fl
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Savanna grasslands (dispersal after molt to higher altitudes)

Acrida sulphuripennis (Gerstäcker, 1869)

Ailopus thalassinus (Fabricius, 1781)

Cataloipus oberthüri oberthüri (Bolivar I., 1890)

Catantops momboensis momboensis Sjöstedt, 1931

Conocephalus (Anisoptera) maculatus (Le Guillou, 1841)

Conocephalus (Conocephalus) conocephalus (Linné, 1767)

Cyrtacanthacris tatarica tatarica (Linné, 1758)

Diabolocatantops axillaris axillaris (Burmeister, 1838)

Duronia chloronota (Stål, 1876)

Gastrimargus africanus africanus (Saussure, 1888)

Gastrimargus determinatus vitripennis (Saussure, 1888)

Oedaleus senegalensis (Krauss, 1877)

Oxya hyla hyla Serville, 1831

Paratettix histricus (Stål, 1861)

Phaeocatantops decoratus decoratus (Gerstaecker, 1869)

Truxalis conspurcata somalia Burr, 1902

Savanna grasslands (undergoing nymphal development also at higher altitudes)

Chrotogonus (Chrotogonus) hemipterus Schaum, 1853

Morphacris fasciata (Thunberg, 1815)

Phaneroptera sparsa Stål, 1857

Zonocerus elegans elegans (Thunberg, 1815)

(+)

(+)

Main habitat	end	fl
Plantation belt (Chagga home gardens)		
Abisares viridipennis viridipennis (Burmeister, 1838)		
Altiusambilla modicicrus (Karsch, 1896)		+
Amytta olindo Hemp, 2001	+	+
Arantia fasciata (Walker, 1869)		
Dictyophorus (Tapesiella) griseus griseus (Reiche & Fairemaire, 1847)		+
Eurycorypha sp.		
Eurycorypha varia Brunner v. Wattenwyl, 1891		
Ixalidium sjöstedti Kevan, 1950		+
Melidia kenyensis Chopard, 1954		
Parepistaurus deses deses (Karsch, 1896)		+
Phymateus (Phymateus) viridipes viridipes Stål, 1873		
Phyteumas purpurascens purpurascens (Karsch, 1896)		
Plangia sp.		
Taphronota (Taphronota) calliparea immaculata Sjöstedt, 1929		
Submontane and montane meadows		
Acanthacris ruficornis ruficornis (Fabricius, 1787)		
Acorypha laticosta (Karsch, 1896)		
Ailopus longicornis Sjöstedt, 1909		
Conocephalus (Xiphidion) kilimandjaricus (Sjöstedt, 1909)	+	+
Coryphosima centralis Rehn, 1914		
Coryphosima stenoptera stenoptera (Schaum, 1853)		
Eucoptacra gowdeyi Uvarov, 1923 Gastrimargus verticalis verticalis (Saussure, 1884)		
Gymnobothroides levipes (Karsch, 1896)		+
Gymnobothrus temporalis temporalis (Stål, 1876)		•
Hadrolecocatantops kilimandjaricus (Ramme, 1929)		
Heteropternis couloniana (Saussure, 1884)		
Horatosphaga heteromorpha Karsch		
Leptacrydium gratiosum (Karsch, 1893)		+
Odontomelus brachypterus (Gerstaecker, 1869)		+
Parasphena meruensis meruensis Sjöstedt, 1909		+
Paratettix villiersi Günther, 1979 Propolia difference (Sorvillo, 1839)		+
Ruspolia differens (Serville, 1839) Ruspolia sp.		
Taramassus cunctator sjöstedti (Ramme, 1929)		
Taramassus cunctator flabellatus (Ramme, 1931)		
Submontane forest		
Horatosphaga montivaga (Sjöstedt, 1909)		+
Parepistaurus lindneri Kevan, 1955		+
Montane forest		
Aerotegmina kilimandjarica Hemp, 2001	+	+
Amytta kilimandjarica Hemp, 2001	+	+
Anthracites kilimandjaricus Sjöstedt, 1909	+	+
Anthracites montium Sjöstedt, 1909		+
Chromothericles kanga (Sjöstedt, 1923)	+	+
Conocephalus (Xiphidion) kibonotense (Sjöstedt, 1909)	+	+
Monticolaria kilimandjarica Sjöstedt, 1909	+	+
Subalpine grasslands		
Parasphena pulchripes (Gerstaecker, 1869)	+	+
Uganda kilimandjarica (Sjöstedt, 1909)	+	+

TABLE 4. Montane and subalpine grasslands on Mt. Kilimanjaro.

Relevé number	5	5	5	1	1	1	4	4	5	5	5	7	7	7	7	7	5	5	5	5	3	3	1	1		4	1 4 0
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Grasshopper plot number	1 8 3	1 8 4	_	2 5	2	2 7	_	_	_	1 8 2	_	_	_	_	_	_	1 9 7	1 9 8	_	_	7 4	7 5	_	_	1 3	1 5 7	1 5 8 -
Grasshopper coenosis	1	1		1	1	1	-	-	-	1	-	-	-	-	-	-	2	2	-	-	2	2	-	-	2	2	2 -
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	3	3	3	2	2	2	2 2	g 2	g 2	2	g 3	g 2	2	2	2	2	1	1	1	1	1	1	1	1	1	g 1	g g
Altitude (10 m asl)	1	2	3	6	6	6	7	8	8	9	0	5	7	7	7	6	7 9	7	7	7	7	6	5	5	6	7	5 5 9 9
Species number Exposition	20	18 s	16 n	18	15 o	15 o	11 so	8 n	15	16 so	12	12	14 o		10 sw		19 sw	29 sw	16 w	20 w	21 sw	28 w	17 o	29 o	25 w	32 w	37 35 w w
Inclination (degrees)	-	5	10	-	10	10	5	10	-	10	-	-	15	20	15	5	25	25	5	25	20	25	30	30	20	20	25 25
Cover herb layer (%, 1x = 100)	60	70	85	40	50	40	80	80	80	50	70	60	70	80	90	90	60	80	50	60	80	85	50	60	60	80	80 80
Height herb layer (dm)	4	4	5	5	4	4	6	6	5	5	5	3	5	5	4	4	4	4	4	4	4	4	3	2	5	5	5 6
Cover moss layer (%)	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	30	20	30	20	20	1	5	5	10	5	0 5
Community number			1	a							1	b										2	a				
							st	ıbal	pine	2																	
Subalpine <i>Festuca</i> grasslands																											
Festuca obturbans	2	2	3	3	1	1	3	3	4	2	2	3	3	2	2	3											
Helichrysum splendidum	2	1	1	1	+	1	1	2	2	1	1			2	1	1											
Bulbostylis atrosanguinea	2	+		+	2	2	1	1	+	1	1																
Koeleria capensis	1	3	:	2	2	2		+	+	1	+		٠	٠	٠			٠	٠		٠		٠	٠	٠	٠	
Cyperus kerstenii	+		1	2	+	+	+	+	+	٠	٠	٠	٠		٠	+		٠		٠	٠	٠	٠	٠		٠	
Aristea alata		+	٠	٠	+			٠	٠	٠	٠	+	+	+	+	+		٠		٠	٠	٠	٠	٠		٠	
Dierama cupuliflorum	+	٠	٠	٠	+	•	•	+	+	٠	+	٠		٠	٠			٠	٠	٠	٠	٠	٠	٠	٠		
Anemone thomsonii	+	1		+	+	+	•			1							١.										
Andropogon amethystinus Wahlenbergia capillacea	1	1	2		r		•			1	÷																
Helichrysum meyeri-johannis	+		Ċ				+		+		+		Ċ	:			1:										: :
1b, subalpine grassland species		_	_	_	_			_	_	_	_	_	_	_	_		1	·	•	•	•	•	•	·	•	·	
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Agrostis producta Thesium kilimandscharicum	•						+		+ r	1	+	+								•		•					
Disa deckenii	•			•	•	•	١.		1	+	1	+	+	+		•	١.			•		•					
Agrostis kilimandscharica							:						1	1	+	1	:										
Ficinia filiformis							`					+	1	+		+	:										
1b + 1a, subalpine + montane	gra	ssla	nd s	peci	ies												1										
Exotheca abyssinica							+	1	+	1	2	2	2	3	3	2	1	2	1	2	2	+	+	+	3	1	2 3
Eragrostis olivacea					1		+	+	+				1	2	3	3	1	1									
Selago thomsonii							+		+			+				+	+	+	+	+							
Blaeria johnstonii							١.					+	1	+	+	+	+	+	1	1							
Helichrysum kilimanjari			+				١.					+	1	+			١.		1	1							
2a, submontane + colline gras	slan	d sp	ecie	s																					_		
Chamaecrista mimosoides																				r						+	+ +
Hyparrhenia hirta								Ċ						Ċ	i		l .		2	+	i		1	1	+		1 .
Wahlenbergia abyssinica																	١.	+						+			+ 1
Sporobolus fimbriatus																	١.							1		+	1 +
Satureia biflora																	١.									2	2 2
Hyparrhenia rufa																	١.								+		1 2
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																	2	2	1	+	1	1	2	1	2	+	1 1
Dry montane <i>Bulbostylis</i> mead									-		-					-	1 -	-	-								
Dry montane <i>Bulbostylis</i> meac <i>Bulbostylis densa</i>																		+			+	+		+	+		
Dry montane <i>Bulbostylis</i> meac <i>Bulbostylis densa</i> <i>Triumphetta rhomboidea</i>			1									+	1	1	+		1	1	1	1	+	1		++	++	1	
Dry montane <i>Bulbostylis</i> meac <i>Bulbostylis densa</i> <i>Triumphetta rhomboidea</i>			1									+	1	1	+		1 2	1 2	1	1	+ , +	+ 1 1	++	+++++	+++++	1	
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Dry montane Bulbostylis meac Bulbostylis densa Triumphetta rhomboidea Helichrysum forskahlii			1										1	1	+		2	2	1 1	1 2	+ , + 2 1	+ 1 1 +	+ + 1	+ + + 1	+ + 2	1 1	

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2b	3
montane	
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Community number				la							_1	Ь								_		2:	a				
							sı	ıbal	pine	e																	
Wet montane Tolpis meadows																											
Monopsis stellarioides																											
Tolpis capensis	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		•	•	•	•	•	•	•	•	•	•
Oldenlandia monanthos																	:										
Cyperus richardii	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		•	•	•	•	•	•	•	•	+	+
Platostoma africanum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		•	•	•	•	•	•	•	•	•	
Poa leptoclada	Ċ		+		Ċ	Ċ			Ċ				Ċ				:										
Wet (sub-)montane meadows																											
Cyperus afroalpinus																	١.				+					+	r
Hypericum peplidifolium		+								+				+												+	+
Cyperus brevifolius			·		·								Ċ		Ċ						Ċ			Ċ			
Eragrostis tenuifolia																	:										
Dyschoriste radicans			·		·					Ċ			Ċ		Ċ						Ċ			Ċ			r
Digitaria thouaresiana			·		·					Ċ			Ċ		Ċ						Ċ			+			
Agrocharis incognita																	[
Veronica javanica																											
Wet colline and (sub-)montan	ie ha	abita	ats	•	•			•	•	•					,		'				,						
Centella asiatica																					1			+			
Cyperus niger elegantulus																	.										
Vigna parkeri																											
Hydrocotyle mannii																											
Digitaria pearsonii	Ċ		Ċ		Ċ				Ċ	Ċ			Ċ		Ċ		[Ċ			Ċ			
Cyperus comosipes decolorans																											
Trifolium usambarense	Ċ		Ċ		Ċ	Ċ			Ċ	Ċ			Ċ				<u> </u>										
Montane meadows																	ı .										
Oldenlandia herbacea																	_	+	_	+	2	2	1	1	1		+
Eragrostis kiwuensis		•	•	•	•	•	•		•		•			•			1	1	+	1	2	2	1	1	1		+
Eragrostis atrovirens	•	•	•	•	•	•	•	•	•		•	•	•	•	•		1	+	•	•	1	1	1	1	+	•	
Spermacoce princeae princeae	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		+	•	•	+	+	•	•	•	•	•
Digitaria abyssinica																						2					
(Sub-)montane meadows																	i i	_	_	_	_	-	_	_	_	_	
																		1			1	1	1	2			
Phyllanthus boehmii humilis		٠	•		•		•				•							1	•						1	+	2
Eragrostis schweinfurthii Richardia scabra		٠	•		•		•				•								•		+	1	1	1	1	2	2 -
Justicia flava		٠	•		•		•				•						1	2	•		+	2	1	1	+	+	+ ·
Crotalaria distantiflora		•	•	•	•	•	•		•		•			•						1	+	1	+	+	+		1
	•	•		•		•		•	•	•	•	•		•		•	+	+	+	r		1	•	+	:	:	
Conyza subscaposa Dichondra repens	•	•		•		•		•	•	•	•	•		•		•		•	•	1	+	•	•	•	+	+	+ -
Alectra sessiliflora		•		•			•				•			•				1	•							+	+
Digitaria longiflora		•	•	•	•	•	•		•		•			•			٠.	1	•	•						+	:
Pseudognaphalium luteo-album		•	•	•	•	•	•		•		•			•			٠.		•	•		+					
Sporobolus piliferus	•	•	•	•	•	•	•	•	•	•	•	•	•	•				•	•	•		1	•	•	1	т	1
Lactuca inermis	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		•	•	•	•	1	•	•	1		+
(Sub-)montane and colline gra	assla	nds	•	•	•	•		•	•	•	•	•	•	•	•	•	i i	÷	_	÷	<u> </u>	÷	÷	·	÷	_	·
Emilia discifolia																	+	+	+		2	2	2	2	+	+	+
Rhynchelythrum repens	•	•	•	•	•	•	•	•	•	•	•	•	•	•			_	1	2	2	+	2	1	1	2	1	1
Companions	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	-	1			т		1	1		1	1
Ageratrum conyzoides																		1			1	,		,	1		2
Conyza sumatrensis				•							•						+	1		٠	1	+		+	1	:	2
Paspalum scrobiculatum				•							•							+				1			+	+	1 .
Sporobolus africanus				•							•										+	1		+		:	+
	٠	٠	٠	٠	•	٠	•	٠	•		•	٠	1			•		٠	1	1	٠	+	•			+	
Pteridium aquilinum		٠	٠	•	+	٠					٠		1	+	+	٠		•	1	1	٠	+		+	+	:	
Commelina spec. Pellaea viridis		٠	٠	•		٠		•		٠	٠	٠	٠	٠		•		+	٠	٠		+	٠		٠	+	
		٠	٠	•		٠					٠		٠		٠				٠		٠			+			+
Helichrysum schimperi	٠	٠	٠	٠	٠	٠		٠	٠		٠	٠		٠			٠.	r		٠	٠					٠	٠

¹a: Subalpine Festuca obturbans tussock grassland, typical subcommunity
1b: Subalpine Festuca obturbans tussock grassland, Exotheca subcommunity
2a: Dry montane Bulbostylis densa meadow, Exotheca subcommunity

	2b	3
	montane	
+ +	+ . + 1 + 1 + + + +	+ + + 2 1 1 1 2 1 1 2 + 1 +
		1 1 1 2 2 2 + 2 1 1 1 2 1 . 2 2 3 1 2 1 + 2 1 1 2 . + + 1 2 1 3 1 . 2
	. +	1 1 2
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	r	2 + 2 . + . + + . 1 1 1 1 + . 1 1 1 1 2 2 2 + . 1 1 1 1 + . 2 + + 2
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r	+	+ r
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1 + . + 1 + . 1 . 1 2 + + + 1 1 + +	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	1 1 + . + 1 + 1 + + 1 . + . 1 1 . + 1 + . 1 1 2 . 2 1 1 + . 2 1 + 2
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	+	+ + + 1 1 1 + + 1 . + 2 + . r

²b: Dry montane Bulbostylis densa meadow, typical subcommunity
3: Wet montane Tolpis capensis meadow
ki = Kidia, kr = Kirua, mc = Machame, mg = Marangu, mu = Maua, mi = Mwika, nj = Nanjara

TABLE 5. Grasshopper coenoses of high-altitude grasslands on Mt. Kilimanjaro.

	,	
Plot number	1 1 1 2 2 2 8 8 8 7 6 5 2 3 4	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
Altitude (m asl)	2 2 2 2 3 3 6 6 6 8 2 1 5 6 9 5 0 2 0 0 0 0 0 0 0	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
Vegetation releve number	1 1 1 5 5 5 4 4 4 2 2 3 3 4 4 3 8 9 2 3	3 4 5 5 2 3 2 5 3 3 3 2 3 3 4 5 1 1 0 0 3 4 3 3 5 3 3 3 2 2 2 4 4 4 0 0 4 3 3 3 3 3 3 3 7 7 5 3 6 7 3 0 5 5 7 5 5 0 8 1 1 1 1 1 3 3 5 2 2 8 2 3 3 7 6 7 3 1 3 3 8 9 3 3 3 3 3 3 6 4 3 4 4 6 8 2 7 6 2 3 0 0 1 2 4 2 3 1 2 2 5 0 7 8 5 9 0 1 2 9 1 8 6 6 7 8 0 9 4 5 7 8
Vegetation community	1 1 1 1 1 1	222222232222222222222223223222333333
Species number	2 4 2 4 3 3	1212111111111111111 111 1 1 1 1 1 1 1 1
Coenosis	1	2 3
	subalpine	montane
Uganda kilimandjarica – Parasphena pulch	a pulchripes coenosis	
Uganda kilimandjarica Parasphena pulchripes	+ + + + + + + + + +	
Parasphena meruensis – Eucoptacra gowd	a gowdeyi coenosis	
Parasphena meruensis Eucoptacra goudeyi Acanthacris ruficomis b Phyreumas purpurascens Ruspolia sp.		+ 2 + + + + + + + + + + + + + + + + + +
Forest edge species		
Parepistaurus deses deses Conocephalus (X) kibonatense Chromothericles kanga Altiusambilla modicierus Amytu olindo		
Submontane and montane meadow spe-	ow species	
Gastrimargus verticalis Acorypha laticosta	· · · · · · · · · · · · · · ·	. 1 + + + + . + . + . + 1 + r + + + + + 1 + 1 + 1 + + + + . + .

																							J
Paratettix villiersi – Lepatacrydium gratiosum coenosis	.sis																						ΙГ
Paratettix villiersi e													:	:	:			+	+	+	3 1 2	7	_
Characteristic species of coenosis 2 + 3																							[
Gymnobothroides levipes Hadroleoccatantop kilimandjarias f Leptacrydium gratiosum		. + .	+ + ·	+ + + + + + + + +	. + .	+ +	+ + +	+ + + +	+ + .	+ · +		. + +	+ · ·	+ · +	· + + + · ·	+ + + +	+ · +	+ + +	+ + +	+ · +	+ + +	- + +	+ +
Companions ((sub-)montane zone)																							
Ixalidium sjöstedti Conocephalus kilimandjaricus		+ +	+ + +	+ +	+ + + +	+ +	+ +	+ + +	+ +		+ +	. +			+ +		+ .		+ +		+ ·	+ +	
Companions (colline to montane zone)																							
Horatosphaga heteromorpha Morphacris fasciata Phaneroptera sparsa		+ + + +	+ · +	+ + + +	+ + + + + + + + + + + + + + + + + + + +	+ + + •	+ + +	+ + + +	· + + + + +	+ + •	+ + + +	+ + +	+ + ·	. + +	. 2 .	+ + ·	+ + ·	+ + •		. + .	+ · +		+
Colline to subalpine grassland species																							
Coryphosima stenopteralcentralis ; . + . + . Heteroptemis couloniana . + . + +	• +	1 2 + + + .	+ +	2 + 1	1 + 1	1 1 +	+ .	+	+	+ +	+ +	+ + 2	1 .	+ + & ·	3 1	2 +	· + + ·	+ •		+ .	. +	+ .	+ .
Companions (submontane species)																							
Odontomelus brachypterus Dictyophorus griseus					+ .					. +	+ ·										. +		
Savanna species																							
Zonocerus elegans Cataloipus oberthuri		+ .	· +		+ .				+ .		+ .	+ ·											
Ruspolia differens		+ -	+ -		+	+	+											٠					
Oedalus senegalensis		· ·	+ +			. +	· +	 	 	 	 			 	 	 	 		 	 			
Phaeocatantops decoratus			+	:			:	:	:					:	:								
vitripennis k		+	:	+														٠					
Conocephatus maculatus		· +																					
Cataloipus oberthuri		+		+		+																	
Autopus tongreornis Conocephalus conocephalus		· · + +		 + +		+ .	 + ·																
Chrotogonus hemipterus Conocephalus maculatus													+ .										
	1																						I

^{1:} Uganda kilmandjarica — Parasphena pulchripes coenosis of subalpine Festuca obturbans tussock grassland
2: Parasphena meruensis — Eucoptacru goudeyi coenosis of dry montane Bulbostylis densa meadows
3: Paratetix villiersi — Lepatacrydium gratiosum coenosis of humid montane Tolpis capensis meadows

isolated savanna hill, still exists as it is regarded as a holy place among the tribe of the Masai. However, changing religious attitudes and increasing population pressure now threaten this tiny forest patch.

Specimens of *Horatosphaga montivaga* were collected from altitudes of 1000–1200 m by Sjöstedt (Ragge 1960) around Kibonoto on the south-western slopes. This species was obtained only within clearings in indigenous forests further west at altitudes of 1300 to 1500 m. In the Kibonoto area no forest is left and has been replaced completely by intensively cultivated banana-coffee plantations. This might be the reason why *H. montivaga* is no longer found there.

Another flightless species indicating narrow microclimatic conditions is the tiny acridid *Gymnobothroides levipes*. It was reported from the savanna to the montane forest border by Sjöstedt (1909), where it has today disappeared in the colline and submontane zone. Nowadays it is exclusively found at altitudes of over 1500 m and occurs on short montane grass-

lands of the southern slopes. On Mt. Kilimanjaro it probably invaded these grasslands, which are only maintained by regular cutting by the local population, from the northern/north-eastern montane/subalpine zone, where it is common and also occurred at lower altitudes (Sjöstedt 1909). Grasslands were created in the (sub)alpine zone by fires, which are a normal phenomenon here, and also because of the frequent grazing by wild animals in the northern parts of Kilimanjaro. Access is much easier from the northern side of the volcano. Here, gorges are shallow and cannot prevent big game from migrating, as is the case on the southern slopes with their numerous inaccessible gorges. Big game probably never played a major role on the southern slopes (Kundaeli 1976), which may be one reason for the totally different structure and plant species composition of the forests. In the same habitat as Gymnobothroides levipes, Parasphena meruensis also occurs, which could also have migrated from the north-eastern subalpine zone to the high-



FIG. 4. Moorland zone above Maua at 2800 m. *Festuca obturbans* grasslands, habitat of the *Parasphena pulchripes* – *Uganda kilimandjarica* coenosis.

altitude grasslands of the southern slopes with the increasing influence of humans by clearing forests.

Table 3 lists all Saltatoria species encountered in the submontane to subalpine zones on the southern slopes of Mt. Kilimanjaro sorted according to their main habitat. Twenty species are savanna forms, most of them restricted with their nymphal development to colline grasslands. Adults then spread into higher altitudes and are found in a variety of habitats. Others, such as *Morphacris fasciata, Chrotogonus hemiptera, Zonocerus elegans*, and *Phaneroptera sparsa* are capable of also coping with lower temperatures for larval development. All these savanna species are indicators of a changed environment from forested to open habitats.

The submontane zone of the southern slopes of Mt. Kilimanjaro is today intensively used for cultivation, and forest is almost absent there. Fifteen species have their main distribution there. Of the 24 flightless species listed in Table 3, only 5 occur in the Chagga home gardens and with Amytta olindo only one endemic is found here. Five species are canopy dwellers. These are Arantia fasciata, Eurycorypha sp., Eurycorypha varia, Melidia kenyensis, and Plangia sp., species which are probably remnants of the former submontane forests. Six flightless species have been recorded from the submontane and montane meadows, with Conocephalus kilimandjaricus as the only endemic. Two species, Horatosphaga montivaga and Parepistaurus lindneri, are restricted to submontane forests and are thus now highly endangered on Mt. Kilimanjaro. Most flightless (7) and endemic (6) species are harbored by the montane forest. The two subalpine species are both flightless and endemic. In the following section the species composition of the highland grasslands is presented, containing most of the species mentioned above for the submontane and montane zones of the southern slopes of Mt. Kilimanjaro.

Saltatoria coenoses of high-altitude grasslands and their relation to vegetation. Table 5 shows the Saltatoria coenoses found in three different grassland associations, which are presented in a parallel vegetation table (Table 4).

1. Parasphena pulchripes - Uganda kilimandjarica - coenosis

The subalpine Festuca obturbans tussock grasslands, with Helichrysum splendidum, Bulbostylis atrosanguinea, Koeleria capensis, and Cyperus kerstenii ("moor-



FIG. 5. The endemic *Parasphena pulchripes* is found up to altitudes of 4500 m.

lands", 2700–3300 m, Table 4, 1a + 1b; Fig. 4) have a completely different species composition from all grassland communities at lower altitudes (cf. Hemp A., 2001). They are separated from the other grassland communities by the montane forest belt that also impedes an exchange of grasshopper species. These grasslands are maintained by fires (Hemp & Beck, 2001).

Restricted to the "moorland zone" are the pyrgomorphid *Parasphena pulchripes* (Fig. 5) and the acridid *Uganda kilimandjarica* (Fig. 6), occurring at rather low population densities.

In addition two widespread grasshopper species are present in coenosis 1. *Coryphosima stenoptera* (species group i in Table 5) occurs in a variety of different grassland types, but becomes more frequent at altitudes of about 1400 m. It is replaced at higher altitudes by the very similar but smaller *Coryphosima centralis*. *C. centralis* has highest abundancies in the *Bulbostylis* meadows, sometimes with more than 5 in-

dividuals per m². It is even found at warm places in the moorland and heathland zones. In Table 5 Coryphosima stenoptera and C. centralis were put together because species status seems to be uncertain. Sjöstedt (1931) described Rodunia deceptor f. kilimana as a synonym of C. centralis (and a smaller form of C. stenoptera), while "normal" and larger R. deceptor (= C. stenoptera) exist with intermediates to the smaller form kilimana. A transect study in the area of Old Moshi, from the savanna to the afroalpine zone, showed the smallest individuals in moorlands at 3200 m. Breeding experiments and/or more detailed population studies are required to show the relationship between C. stenoptera and C. centralis.

The oedipodine *Heteropternis couloniana* is also distributed over a wide range on Mt. Kilimanjaro. Similar to the eurosiberian acridine *Stethophyma grossum* (Linné, 1758), males of *H. couloniana* produce



FIG. 6. The endemic acridine *Uganda kilimandjarica* is restricted to grass- and heathlands of the Afroalpine zone.

cracking noises with their tibiae. This species, being widely distributed in Africa south of the Sahara (Dirsh 1965), is strongly geophilous and thus restricted to open places (Phipps 1966, Dirsh 1970, Hochkirch 1996). Sjöstedt (1909) recorded this oedipodine from the savanna to the afroalpine zone on Mt. Kilimanjaro. At Mt. Elgon it inhabits elevations of 1700 to 4000 m (Uvarov 1938) and in Cameroon it was found at an elevation of 2000 m on Mt. Bambouto (Chopard 1945). Its main habitat is the high-altitude grasslands where the species reaches high constancies

and builds up populations of more than one individual per m² on the southern slopes of Mt. Kilimaniaro.

The typical Festuca obturbans grasslands (1a) and Festuca grasslands with Exotheca abyssinica (1b) are intermingled at the same altitudes and localities. These units are very similar in species composition and structure. Only one grasshopper plot could be established in subcommunity 1b, which showed no difference with plots in the other subcommunity.

2. Parasphena meruensis-Eucoptacra gowdeyi-coenosis of the Bulbostylis meadows

At altitudes of 1600 to 1900 m on the southern slopes of Mt. Kilimanjaro the former forest belt is replaced, due to human activity, in certain areas by mowed meadow communities characterized by sedges and grasses like Bulbostylis densa, Cyperus pseudoleptocladus, and Digitaria abyssinica and herbs like Helichrysum forskahlii and Anisopappus oliveranus (Bulbostylis meadows, Table 4, 2a + 2b, Hemp, A. [2001], Fig. 7). Only slightly different in plant species composition are Bulbostylis meadows with Exotheca abyssinica (Table 4, 2a). In this unit plant species of the subalpine Festuca obturbans tussock grassland such as Exotheca abyssinica, Eragrostis olivacea, and Selago thomsonii occur as well as species from colline and submontane grasslands, e.g., Hyparrhenia hirta and Wahlenbergia abyssinica.

The pyrgomorphid Parasphena meruensis and the coptacridine Eucoptacra gowdeyi (species group b, Table 5) are species restricted to this coenosis on Bulbostylis meadows (coenosis 2). Both species are very rarely found lower than 1400 m on the southern slopes of Mt. Kilimanjaro. Parasphena meruensis was described from both Mt. Meru and Mt. Kilimanjaro by Sjöstedt (1909). He recorded this species on Mt. Kilimanjaro from the plantation belt while on Mt. Meru it was found in montane forest at 3000-4000 m. While the montane forest on Mt. Kilimanjaro, undisturbed by big game, densely encircles the whole western, southern, eastern and parts of the northern slopes, on Mt. Meru the forest is strongly influenced by the abundant buffalo. Meadow patches are found into high altitudes providing habitat for Parasphena meruensis. On Mt. Kilimanjaro game is an important factor only on the northern side. Above Rongai huge grasslands, created by intensive grazing by game, have developed above the forest, where Parasphena meruensis builds up high population densities and has been



FIG. 7. Bulbostylis meadow above Kidia at 1710 m.

noted to elevations of over 2500 m. *Eucoptacra gow-deyi* is a species distributed over East Africa to Zambia and Zaire (Dirsh 1965). Miller (1925) found it in southern Tanzania at altitudes of about 1500 m.

A copiphorine of the genus Ruspolia also has its main habitat in the Parasphena meruensis-Eucoptacra gowdeyi-coenosis. At lower altitudes it is replaced by the larger Ruspolia differens whose hoppers were never found higher than 1400 m. When adults emerge, Ruspolia differens spreads to altitudes of more than 1800 m and is then found in the same habitat as the smaller Ruspolia sp. Due to the "El Niño" rains in 1997/98 R. differens developed huge swarms in March 1998, probably originating in savanna grasslands, damaging crops in the plantations of the southern slopes of Mt. Kilimanjaro. The swarming behavior of this species has been recorded in detail by Bailey & McCrae (1978) in Uganda, where swarms of Ruspolia differens are a common phenomenon.

The nymphs of *Acanthacris ruficornis ruficornis* are commoner in more mesophilic meadow patches from October to January while the adults inhabit bushes

and small trees, remnants of the former forest that are scattered into the grasslands. In January, when first adults of this species appear, this flight-active cyrtacanthacridine spreads also to lower altitudes, even reaching savanna grasslands.



FIG. 8. The hoppers of *Phyteumas purpurascens* develop on the high-altitude meadows while the adults prefer bushes at the same altitudes.



FIG. 9. The oedipodine *Gastrimargus verticalis verticalis* inhabits submontane and montane meadow communities.

Phyteumas purpurascens (Fig. 8) is a common species on the open meadow patches at altitudes of 1700–1900 m. Nymphs and adults of this large pyrgomorphid are found here on bushes and small trees. At lower altitudes *P. viridipes*, which resembles *Phyteumas purpurascens* in shape, color and size, occurs on bushes in the plantation belt but is infrequently also found on the high-altitude meadows.

Common in submontane grasslands at lower altitudes are widespread species such as the oedipodine



FIG. 10. The endemic *Chromothericles kanga* prefers clearings and forest edges where it is often found on *Rubus steudneri*.

Gastrimargus verticalis (Fig. 9) and the calliptamine Acorypha laticosta (species group d in Table 5). On Mt. Kilimanjaro G. verticalis was recorded from the savanna to the plantation belt on the south-western slopes by Sjöstedt (1909), and on the western, southwestern, and south-eastern slopes from elevations of 1200 to 1900 m by Ritchie (1982). On the southern slopes it occurs only in submontane grasslands above 1200 m where it is very abundant at elevations of about 1400 m. But it also has high constancies in Bulbostylis meadows and builds up dense populations of up to one individual per m2 (see Table 5). Below 1200 m G. verticalis is replaced by the savanna species G. africanus. Acorypha laticosta is known from Zimbabwe, Malawi, and Tanzania (Jago 1966). Sjöstedt (1909) collected this species on south-western and northern Kilimanjaro from the savanna to the plantation belt up to an altitude of 1800 m, and Jago (1966) in the same area from 1200 to 1500 m. On the southern slopes it occurs in submontane grasslands above 1300 m to high-altitude grasslands (Table. 4).

Above Kirua (plots 40 to 44, 70 to 74) the montane forest has been completely destroyed near the village. Wide open grasslands prevail, which are intensively cut by the locals and are also used sometimes as grazing grounds for cattle. Here only single bushes remain. Species such as Parepistaurus deses, Altiusambilla modicicrus, Ixalidium sjöstedti, Conocephalus kilimandjaricus, and C. kibonotense, which prefer lush herbs along forest edges or near bushes and small trees, are lacking here. For Chromothericles kanga, which favors clearings in forest disturbed to a certain degree, the air humidity is too low on the single bushes of the grasslands above Kirua. On the other hand, highest species diversity is found on meadow patches that are inside montane forest, for example above Kidia (plots 1, 2, 24, 66, 69, 86 to 89, 134), the Msaranga valley (plot 75, 78), or Mbokomu (plots 197 to 199). The habitats range here from closed forest to open to varying degrees forests to short-cut grasslands. In such areas flightless forest-edge species (species group c) occur in coenosis 2, increasing the species numbers significantly. Species like Chromothericles kanga (Fig. 10), Acanthacris ruficornis, Eurycorypha sp., and Phyteumas purpurascens inhabit the bushes scattered to the grasslands or prefer sunny forest edges. If the bushes and trees are denser, typical forest species become dominant, such as Monticolaria kilimandjarica, Amytta olindo, and Melidia kenyensis. In disturbed but closed forest Anthracites montium, and A. kilimandjaricus, Aerotegmina kilimandjarica (Hemp, C. 2001a) and Amytta kilimandjarica (Hemp, C. 2001b) inhabit the tree layer.

The Mt. Kilimanjaro endemic Conocephalus kilimandjaricus (species group g) is usually associated with more humid habitats, like swamps or along lowaltitude riversides in the submontane zone, where it reaches abundancies of more than five individuals per m². But this flightless species inhabits montane Bulbostylis and Tolpis meadows as well and follows grassy paths in montane rain forest, where it is replaced by the endemic Conocephalus kibonotense. The tetrigid Leptacrydium gratiosum is regularly found in all open land communities between 1250 and 1800 m. The flightless catantopine Ixalidium sjöstedti has its main habitat at lower altitudes of 1300 to 1400 m. At higher elevations this species leaves the semi-shade and finds adequate habitats also in montane meadows though is still found in the litter along forest edges.

The typical Bulbostylis meadows (2b) and Bulbostylis meadows with Exotheca abyssinica (2a) are intermingled at the same altitudes and localities at 1600-1900 m. These units are formed by the slightly different exposition of the sites and occur together in many cases. Generally no differences in the Saltatoria inventory was noted in these plant subcommunities. Two vegetation relevés (268 and 272) of coenosis 2 belong to the Tolpis meadows, the habitat of coenosis 3. As can be seen from the vegetation table, these two plots have an intermediate stage between the drier Bulbostylis and the wetter Tolpis meadows, indicated by the species Bulbostylis densa, Triumphetta rhomboidea, and Helichrysum forskahlii. Otherwise all grasshopper plots of coenosis 2 belong to the Bulbostylis meadows.

3. Paratettix villiersi-Leptacrydium gratiosum-coenosis of Tolpis meadows

The more humid *Tolpis* meadows (Tables 4, 3; Fig. 11), often on riversides, are characterized by *Tolpis* capensis, Oldenlandia monanthos, Monopsis stellarioides, Cyperus brevifolius, and C. afroalpinus. As in case of the Bulbostylis meadows, *Tolpis* meadows were created by the clearing of indigenous montane forest and are maintained by the local population by collecting grass as food for their lifestock.

The Paratettix villiersi-Leptacrydium gratiosum-coenosis is characterized by the name-giving species which reach a constancy of 100%. Especially Paratettix villiersi builds up very high population densities of more than 5 individuals per m² on the humid, short grasslands. In the Paratettix villiersi-Leptacrydium



FIG. 11. *Tolpis* meadow of a small river above Maua (1800 m).

gratiosum-coenosis several cricket species occur at high population densities.

Characteristic Saltatoria species common to both montane coenoses 2 and 3 are *Gymnobothroides levipes* and *Hadrolecocatantops kilimandjaricus* (Fig. 12, species group f). The catantopine *Hadrolecocatantops kilimandjaricus* occurs in the Kilimanjaro-Meru area and on the adjacent Chyulu hills (Ramme 1929, Kevan 1950). From collection material *H. kilimandjaricus* is reported even from altitudes of 2700 m on the Kifinika hill on Mt. Kilimanjaro (Jago 1994).

Morphacris fasciata (species group h) is a common species all over Africa (Dirsh 1965). This geophilous species indicates disturbed places and reaches high abundancies in open localities with sparse vegetation. A wide array of grassland habitats is populated by the phaneropterids *Phaneroptera sparsa* and *Horatosphaga heteromorpha*. Nymphs and adults of these two katydids were recorded from all grasslands investigated from 900 to 1900 m.



FIG. 12. The catantopine *Hadrolecocatantops kili-mandjaricus* is known from Mt. Kilimanjaro, Mt. Meru, and the Chyulu Hills.

The pyrgomorphid Zonocerus elegans (species group k) occurs in a wide range of habitats. Clustered L1-nymphs were found on cultivated fields in the savanna region (800-1000 m) as well as in the whole of the plantation belt (1000-1700 m) including the high-altitude grasslands. Nymphs and adults can be found year round. In December and January many species from lower altitudes (800-1200 m) molt to adults and disperse to higher altitudes on the southern slopes of Mt. Kilimanjaro. The huge cyrtacanthacridine Cyrtacanthacris tatarica, whose nymphs are common in various savanna grasslands, spreads in great numbers over the plantation belt and is even capable of passing the montane forest belt. It was seen at altitudes of about 3500 m in the heathlands of the afroalpine zone of Kilimanjaro. Other species are blocked by the forest belt, but can be found after the adults have molted as high as the high-altitude grasslands, e.g., Oedaleus senegalensis, Gastrimargus africanus, Conocephalus maculatus, or Acrida sulphuripennis. Studies on the species C. maculatus showed that nymphs died at constant temperatures of 15°C, and had problems in molting at temperatures below 20°C (Oda & Ishii 1998). In a transect study from the savanna to the montane forest border, nymphs of this species were found up to submontane grasslands at altitudes of about 1200 m. Some last nymphs were obtained at an altitude of 1350 m on short-cut meadow slopes, while adults were infrequently noted to elevations of about 1800 m.

CONCLUSIONS

The phytosociological classification and the classification of grasshopper coenoses are almost identical. As in temperate zones, the grasshopper communities on Mt. Kilimanjaro seem to be strongly dependent on the local plant associations, mainly a result of the typical microclimates arising from a combination of structural (vegetation cover and height), topographic (altitude, exposition, inclination) and climatic (temperature) parameters (cf. Hemp & Hemp 2000).

Absence or presence of Saltatoria in Table 5 are, in addition to these parameters, also a result of the frequency of cutting of the grasslands by the locals. Intensively used grasslands, e.g., near villages, generally show a lower species diversity and species like *Morphacris fasciata* occur at high population densities. High population densities of widely distributed savanna species indicate the degree of destruction of a habitat. Open patches devoid or sparse in vegetation favor euryoecious savanna species.

The study of the habitat requirements of Saltatoria species as presented in this paper enables ecologists to make predictions about the degree of disturbance of an area (bioindication), such as in comparing the proportion of euryoecious savanna species in a habitat with that of stenoecious species. From the percentage of widely distributed "savanna" species to locally restricted more or less endemic species, an indicator is found for evaluation habitat quality and landscape changes can be reconstructed. At present, due to logging and increasing human population pressure, large areas of forest are lost and transformed into farmland. This process is documented by the Saltatoria species, since savanna species penetrate into areas where locally restricted species formerly were in the majority, indicating microclimatic changes.

On the other hand, present distribution and detailed habitat requirements help us to understand the mechanisms of speciation, which has led to the evolution of so many high-mountain endemics in African families and genera such as Parasphena, Parepistaurus, Ixalidium, Aerotegmina, Lentulidae, and Eumastacidae. Regionally confined habitats, such as those along climatic and altitudinal gradients on high mountains (e.g, Eastern Arc Mts., Mt. Kilimanjaro, Mt. Meru/Monduli, Mt. Kenya, Mt. Elgon) are characterized by many locally restricted species. One cause of their speciation might be constant climatic conditions and isolation from each other (Rodgers & Homewood 1982), as well as climatic fluctuations creating migration corridors for stenoecious species spreading from geological old ridges to young volcanoes. The altitudinal gradient, especially on high massifs like Mt. Kilimanjaro, creates numerous habitats and might have favored adaptive radiation for arriving species by the presence of unoccupied niches.

When the ancestors of the flightless genus Parasphena expanded their ranges, montane grasslands must have prevailed in East Africa since all members of this genus have the same habitat requirements. The results on Mt. Kilimanjaro show the close relationship of Parasphena meruensis and P. pulchripes to montane and (sub)alpine grasslands. An "arrival" of Parasphena ancestors may have occurred twice at Mt. Kilimanjaro, which is thought not to be older than 1.5 M years (Downie & Wilkinson 1972). P. pulchripes is endemic to Mt. Kilimanjaro. Nowadays it occurs syntopically with P. meruensis on the northern sides of Mt. Kilimanjaro. P. meruensis prefers altitudes of 1500 to 1700 m, reaching its upper limit of occurrence at about 2700 m on the northern side of Mt. Kilimanjaro, which is the lower limit of *P. pulchripes*. This suggests, especially as P. meruensis has further subspecies on adjacent mountains and occurs with the same subspecies also on Mt. Meru, that it arrived at a later time, when *P. pulchripes* had already speciated. That open habitats always played a major role on Mt. Kilimanjaro can thus be seen in the presence of endemic species in this region. Fires are probably the most important natural factor (Hemp & Beck, 2001) keeping certain areas of the montane and subalpine area constantly open to allow the speciation of open habitat species. This theory is sustained also by the endemic Uganda kilimandjarica. Only two more species of *Uganda* are known, occurring locally restricted in Kenya and Uganda. Thus the climate must have been colder and drier than today when the ancestors of Parasphena spread. Allopatric species of Parasphena are known from most volcanoes (Mts. Kilimanjaro and Meru, Mt. Kitumbeine, Mt. Elgon) and old base mountains like Chyulu Hills, Taita Hills, or Ngong Hills.

When the forest edge species *Parepistaurus* expanded, forests must have provided corridors for migration. *Parepistaurus* is known from coastal forests to submontane and montane forests of the Eastern Arc Mts. to the "young" volcanoes Mt. Kilimanjaro and Mt. Meru as far as the highlands around Nairobi. *Parepistaurus* species are lush vegetation dwellers, preferring clearings and forest edges (Green 1998). When *Parepistaurus* reached Mt. Kilimanjaro the area must have been more forested than at present since the open savanna prevailing today would empede its spread.

Members of the Lentulidae are known to have their diversity center in southern Africa (Jago 1981), most of them being forest species. Thus they have probably spread via forests as far as East Africa and are found here from coastal forest (Hemp, unpubl. data) to montane areas. When their ancestors reached Mt. Kilimanjaro at a time when it was perhaps more humid with a greater forest cover, rapid speciation took place since the species found today on Mt. Kilimanjaro and Mt. Meru is regarded as belonging to the monotypic genus *Altiusambilla*.

The study of the detailed habitat requirements of locally restricted species and their biogeographic distribution pattern are thus very helpful in understanding the climatic history and the mechanisms of speciation in East Africa.

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