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Source: Journal of Orthoptera Research, 16(1): 85-96

Published By: Orthopterists' Society

URL: https://doi.org/10.1665/1082-6467(2007)16[85:NLSFEA]2.0.CO;2

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New Lentulidae species from East Africa (Orthoptera: Saltatoria)

Accepted March 20, 2007

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Abstract

New species of *Rhainopomma* and of *Altiusambilla* from the northern part of the Eastern Arc mountains of Tanzania are described, based on morphological, molecular and geographical data. Ancestors of the genera *Usambilla, Rhainopomma* and *Altiusambilla* probably spread when a different climatic regime favored forest cover connecting presently isolated high mountains of East Africa. After forests retreated, allopatric speciation was the driving force resulting in the biographical pattern of closely related lentulid species we see today in the Eastern Arc mountains and inland volcanoes of Tanzania and Kenya.

Key words

Orthoptera, Lentulidae, Rhainopomma, Altiusambilla, new species, East Africa, Tanzania, Kenya

Introduction

The Lentulidae comprise a small acridoid family mainly distributed over southern Africa (Dirsh 1956, 1965; Brown 1959, 1960, 1962). Little is known about their ecology. Five genera have their centers of diversity in East Africa, of which species of three genera were recently investigated genetically (Schultz *et al.*, 2007). The three investigated genera—*Usambilla*, *Rhainopomma*, and *Altiusambilla* proved closely related to each other, while clearly separated from South African genera such as *Karruia*, *Lentula* and *Eremidium*.

Probable evolutionary events are interpreted by Schultz *et al.* as follows: East African Lentulidae descended from a branch of lentulids that spread from southern Africa, their likely area of origin, over highland ranges to East Africa. Here an adaption to tropical climate occurred. In particular *Rhainopomma* underwent rapid speciation on isolated mountains with montane forest. The sister group to *Rhainopomma* is *Usambilla*. *Altiusambilla* is the sister group to *Usambilla* and *Rhainopomma*. Morphological resemblance especially between *Altiusambilla* females and females of various *Rhainopomma* species is due therefore to convergent evolution (Schultz *et al.* 2007), as already suggested by Jago (1981).

In the present paper ecological data of East African Lentulidae are presented and new species described for *Rhainopomma* and *Altiusambilla*, based on their distribution, habitat, morphology and phylogenetic relationship.

Material and Methods

Identification.—Rhainopomma and *Altiusambilla* species were identified with keys of Jago (1981). The material was checked again in the entomological collection of the National Museums of Kenya, Nai-

robi, at the Natural History Museum, London, and the Naturkunde Museum, Berlin.

Collection plots.—Habitat analyses recording vegetation, altitude and co-occurring Saltatoria were made along the northern part of the so-called Eastern Arc mountains of Tanzania and southern Kenya, as well as on the volcanoes Mt Kilimanjaro, Mt Meru and Mt Kenya, focusing on known and potential habitats for *Rhainopomma* and *Altiusambilla* species (Table 1).

Depositories.— MNB: Museum für Naturkunde, Zentralinstitut der Humboldt-Universität zu Berlin. NHML: Natural History Museum London, UK. EDNMK: Entomological Department National Museums of Kenya, Nairobi. All other material remains in the collection of the senior author.

Genetic analyses.—For 10 *Altiusambilla* specimens and 23 *Rhainopomma* specimens from different locations, a 499 bp fragment of mitochondrial 16s rDNA was sequenced to detect the phylogenetic relationships within these clades. Based on the molecular data, different tree reconstruction methods (Distance, Maximum Likelihood and Maximum Parsimony) agree in a stable phylogeny of the observed taxa (Schultz *et al.* 2007). All sequences were deposited at the NCBI Genbank under the following accession numbers: *Altiusambilla* DQ523690 – DQ523699, *Rhainopomma* DQ523700 – DQ523722.

Results

Five *Rhainopomma* taxa were investigated for their distribution, their habitat demands and altitudinal span. Their phylogenetic relationship based on molecular data separates the observed specimens into five distinct groups, indicating species status prompted by their morphology and biogeography: *Rhainopomma montanum* (Taita Hills), *Rhainopomma magnificum* (South Pare), *Rhainopomma usambaricum* (East Usambara) and two species unknown to science, *Rhainopomma* n. sp. (North Pare) and *Rhainopomma* n. sp. (West Usambara). The phylogenetic relationships of *Rhainopomma* are shown in Fig. 2. High bootstrap values (1000 replicates) between groups and low values within groups indicate a good phylogenetic signal within the data (Wägele 2005), supporting the species level indicated by the morphological and ecological investigations.

Two *Altiusambilla* taxa were observed for their distribution, habitat demands and altitudinal span. The results based on molecular data (Schultz *et al.* 2007) show two distinct groups within this genus

Species	Area
R. usambaricum (Ramme 1929)	Tanzania, East Usambara Mts., Zigi trail, Amani area (Kwamkoro forest reserve)
R. montanum (Kevan 1950)	Kenya, Taita Hills, Wundanyi area, Ngangao forest reserve
R. magnificum Jago 1981	Tanzania, South Pare, Mt Shengena, Kisiwani area, Gonja area, Duma area
R. uguenoensis n. sp.	Tanzania, North Pare, Mt Kindoroko, Kiverenge Hill, Uchame area, Ngofi forest reserve
R. pseudomontanum n. sp.	Tanzania, West Usambara, Mt Kwagoroto, Mazumbai forest reserve, Gogoi forest reserve, Lushoto disturbed forest
A. modicicrus (Karsch 1896)	Tanzania, Mt Kilimanjaro, Mt Meru, Monduli Range
A. keniensis n. sp.	Kenya, Mt Kenya, Chogoria route

Table 1. Collection localities of Rhainopomma and Altiusambilla species.

indicating species status: *Altiusambilla modicicrus* (Mt Kilimanjaro and Mt Meru) and a species unknown to science *Altiusambilla* n. sp. (Mt Kenya). The molecular results are given in Fig. 9., with high bootstrap values (1000 replicates) between groups and low values within groups, supporting the phylogenetic relationships illustrated there. Further investigation of *Altiusambilla modicicrus* from Mt Meru might reveal subspecies or even species among the lentulids occurring on the two volcanoes Mt Meru and Mt Kilimanjaro (Fig. 9).

Habitats

Rhainopomma species are dwellers in herbaceous vegetation. Most species are restricted to single mountains of the Eastern Arc complex. *R. montanum* from the Taita Hills and *R. pseudomontanum* n. sp. from the West Usambara mountains are confined today to the montane zone of the mountains, while *R. magnificum* from the South Pare Mts and *R. uguenoensis* n. sp. from the North Pare Mts, occupy forest and forest edges of a wider altitudinal span, from the colline to the montane zones of the mountain ranges. *Altiusambilla modicicrus* from the Mt. Kilimanjaro-Meru area was recorded in submontane and montane plantations, in submontane and montane forests and forest edges from 1300 to 2800 m (Hemp & Hemp 2003, Hemp 2005). Sjöstedt (1909) recorded *A. modicicrus* at altitudes of 3000 to 3500 m in the montane forests of Mt Meru. On the Monduli range this species was found in montane forest and forest edge from 2000

m (the lower border of forest) to about 2400 m. *A. keniensis* was hitherto collected only in one area on Mt Kenya (Chogoria route), in disturbed montane forest from the lower border of the forest at about 1700 m to about 2000 m (Table 2).

On Mt Meru, Mt Kilimanjaro and the North Pare Mts *A. modicicrus* and *R. uguenoensis* n. sp. have adapted to anthropogenic habitats such as the coffee-banana plantations, as long as these provide lush herbaceous vegetation. The coffee-banana plantations, replaced continuously, resemble in many respects the former submontane forest, which is the reason that many submontane elements of flora and fauna survive in these highly anthropogenic-influenced landscapes (Hemp A. 2005, Hemp C. 2005).

Phylogenetic relationship

The phylogenetic relationship of various *Rhainopomma* and *Altiusambilla* species is presented in Schultz *et al.* 2007. Analyses showed, that *R. montanum* from the Taita Hills is distinctly separate from the species found in the West Usambara Mts. Both species were listed as one species by Jago (1981). Although morphologically hardly distinguishable, *R. montanum* from the Taita Hills and *R. pseudomontanum* n. sp. from the West Usambara Mts are not closely related. The sister species to *R. pseudomontanum* n. sp. is *R. usambaricum* from the adjacent East Usambara Mts.

Rhainopomma samples from the North Pare Mts, collected from

Table 2. Data on distribution, habitat and altitudinal range of Rhainopomma and Altiusambilla species.

Species	Locality	Habitat	Altitudinal range
R. usambaricum	East Usambara	submontane forest and forest edge	450 to 1000 m*
R. montanum	Taita Hills	in forest clearings (Kevan 1950) disturbed montane forest, montane forest and forest clearings, forest edge	1370 to 1680 m, (Kevan 1950) 1470 to 1750 m
R. magnificum	South Pare	colline to submontane riverine forests, submontane forest and forest edge, montane forest and forest clearings	640 to 2200 m
R. uguenoensis n. sp.	North Pare	submontane and montane banana-coffee plantations, submontane and montane forest and forest edge, montane forest clearings	1300 to 1950 m
R. pseudomontanum n. sp.	West Usambara	montane forest and forest edge	1800 to 2000 m**
	Mt. Kilimanjaro	riverine forests, banana-coffee plantations, submontane and montane forest and forest edge, montane bushland	1300 to 2800 m
A. modicicrus	Mt. Meru	montane forest and forest edge	2000 to 3500 m (Sjöstedt 1909 data and data of CH)
	Monduli range	disturbed montane forest and forest edge	2000 to 2400 m
A. keniensis n. sp.	Mt. Kenya	disturbed montane forest and forest edge	1700 to 2000 m

* Kevan (1950) recorded *R. usambaricum* from the Shimba Hills of Kenya but states that without having checked authentic material he could not be sure that the specimens he collected on the Shimba Hills were the same as those described from the Usambaras.

**Jago (1981) reported *R. montanum* from Gonja forest reserve at an altitude of about 640 m in the northern foothills of the South Pare Mts. Specimens collected at the Gonja forest reserve and genetically screened all belonged to *R. magnificum*.

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1400 to 1950 m, clustered together as a separate species, being the sister taxon to *R. pseudomontanum* of the West Usambaras and *R. usambaricum* of the East Usambaras (Fig. 2).

Rhainopomma pseudomontanum Hemp n. sp.

Holotype male.— Tanzania, West Usambara mountains, 1800 m, montane forest edge, Kwagoroto forest reserve, 3/03; Hemp coll.; depository, MNB.

Paratypes.— 3 males, 5 females, all Tanzania, same data as holotype; 7 males, 7 females, West Usambara Mts, 1530 m, Mazumbai forest reserve, open tea plantation at lower border of forest, on herbaceous vegetation along irrigation canal at same altitude and on herbaceous vegetation along forest path at 1550 m, 10/06 and 1/07. Depositories: 1 female, MNB; 1 male, 1 female, NHML; 1 male, 1 female, EDNMK; all other material remains in the collection of the author.

Description.— Male: Color: brownish with a little green. Head and antennae: [as described by Jago (1981) for *R. montanum*] antennae green to dull brown with segments 8 and 12 lighter in color, cream or greenish (Fig. 13, Pl. II). Head dark to light brown; behind eyes dorso-lateral cream band that continues over pronotum; compound eyes very globose (Figs 12, 13, Pl. II). Thorax: lower part of sides of pronotum with conspicuous cream band, bordered above by darker brown to black lateral fasciae continued laterally over abdomen; pronotum dorsally with lighter brown fascia, continued over whole of abdomen. Legs: as in *R. montanum*, green to brownish, posterior femora mostly green with knees brown; posterior tibiae green, apical ends brown; posterior tibiae with two dorsal rows of stout white spines with black tips. Abdomen: subgenital plate brown or green; supra-anal plate brown, callosities (denticles) marked black (Fig. 1); cerci green or brown with darker tips.

Female: General facies: color brown and green, habitus more stout than male (Fig. 14, Pl. III). Thorax: cream lateral fascia, starting as in male behind eye, but not as conspicuous, color more dull; dark brown lateral fascia only on lateral lobes of pronotum, ending with beginning of abdomen, this lateral fascia appearing again with segment three of abdomen.

Measurements (mm).-

R. pseudomontanum	males $(n = 4)$	females $(n = 5)$
head width	2.8 to 2.9	3.4 to 3.5
interocular distance	0.2	0.5 to 0.6
pronotum	2.0 to 2.3	3.5 to 3.7
posterior femur length	6.5 to 6.7	8.2 to 8.7
posterior femur depth	1.7	2.0 to 2.2
total body length	9.5 to 10.5	15.5 to 16.5

Diagnosis.— Morphologically very similar to *R. montanum* from the Taita Hills the name under which it was placed by Jago (1981); However, *R. montanum* is more brightly colored, the cream to white fascia on head and pronotum much more conspicuous; in *R. pseudo-montanum* the upper dorsal cream fascia is small, reduced to a line, while this band is very apparent in most *R. montanum* individuals. The eyes appear much more globose, the head is more constricted in the neck in *R. pseudomontanum* than in *R. montanum* (eye separation at the head's largest diameter:eye separation at neck: 1.32 to 1.36 in *R. pseudomontanum*, 1.15 to 1.23 in *R. montanum*); also in females the eyes are more globose in *R. pseudomontanum* than in *R.*

montanum. Most individuals of *R. pseudomontanum* have six callosities on their supra-anal plate (rarely 5 or 7), while *R. montanum* has mostly eight callosities (rarely 7). Molecularly the two species are clearly separated: *R. montanum* stands at the base of all investigated *Rhainopomma* species [Schultz *et al.* 2007]. This separation accords with the geographical distance between the Taita Hills and the Pare and Usambara Mts (Fig. 2, see map Fig. 10).

Rhainopomma uguenoensis Hemp n. sp.

Holotype male.— Tanzania, North Pare Mts., 1600 m, herbaceous undergrowth of banana-coffee plantation, Mt. Kindoroko, 9/02; Depository: MNB.

Paratypes.— 1 female, forest edge Mt. Kindoroko, 1750 m, 4/01, Depository MNB; 1 male, same data as holotype, Depository NHML; 1 female, Mt. Kindoroko, forest edge, 1750 m, 4/01, Depository NHML; 1 male, 1 female, Mt. Kindoroko, forest clearing, 1800-1870 m, 2/01, Depository EDNMK; all other material remains in the collection of the author.

Additional material examined.— 54 males, 40 females, 8 nymphs, Mt. Kindoroko, lower forest border, herbaceous vegetation at forest edge, 1750 m 2/01, 4/01; Mt. Kindoroko, riverine forest patch, 1570 m, 3/01; Mt. Kindoroko, banana-coffee plantation, 1550 m, on herbaceous vegetation, 6/04; Mt. Kindoroko, banana-coffee plantation, 1600 m, on herbaceous vegetation, 9/02; Kiverenge Hill, 1400 m, disturbed submontane forest, on forest clearings on herbaceous vegetation, 1/05; Kiverenge Hill, 1620 m, montane forest, in small forest clearing on herbaceous vegetation, 1/05; Uchame area, small patch of submontane forest, on forest floor, 1700 m, 9/01; between Ghogo and Butu, banana-coffee plantation, 1300 m, 9/01; Ngofi forest reserve, herbaceous vegetation at lower border of forest, 1600 m, 10/06 and 1/07.

Description.— Male:

Color: vivid green with black and yellow. Head and antennae: cuticle sculptured; antennae greenish at base becoming dark brown to black apically; segments 8 and 12 sometimes lighter in color, apical segment conspicuously white (Fig. 15, Pl. III); head a pattern of black and yellow: eyes encircled yellow, from here lateral yellow fasciae originate being continued over pronotum and abdomen. (Fig. 15, Pl. III); compound eyes black; elevated margins of fastigium verticis yellow, central area black. Thorax: cuticle sculptured; dorsolateral and lateral yellow fasciae. Legs: vivid green, knees of hind femora light brown; hind tibiae greenish-bluish, especially in living insect



Fig. 1. Male supra-anal plate of *R. pseudomontanum* n. sp.



Fig. 2. Molecular phylogeny of *Rhainopomma* species based on DNA sequences from the mitochondrial 16S rDNA locus. Bootstrap values (1000 replicates) at nodes in the order: distance, ML, MP. "*" for nodes not resolved.

more bluish, fading in preserved insect; hind tibiae with white stout spines, tipped black; tarsae also slightly bluish, in preserved insect more tawny. Abdomen: lateral yellow fascia continued to third abdominal segment, dorsolateral fascia to about fourth abdominal segment; abdomen more brownish, sternites of abdomen greenish; posterior end of abdomen greenish-bluish; callosities of supra-anal plate black (Fig. 3); cerci greenish to brown.

Female.—General facies: color more dull than in males, more brown than green. Thorax: yellow lateral fascia not as conspicuous as in male, color more yellow-cream (Fig. 16, Pl. III); hind femora often brown.

Measurements (mm).—				
R. uguenoensis	males $(n = 10)$	females $(n = 10)$		
head width	2.9 to 3.5	3.5 to 4.5		
interocular distance	0.2 to 0.3	0.5 to 0.7		
pronotum	2.1 to 2.4	3.2 to 4.3		
posterior femur length	6.2 to 7.3	8.3 to 10.8		
posterior femur depth	1.6 to 2.1	2.1 to 3.0		
total body length	9.8 to 13.8	14.0 to 19.2		

Diagnosis.— The supra-anal plate of male *R. uguenoensis* resembles that of *Rhainopomma montanum* and *R. pseudomontanum* in respect to



Fig. 3. Male supra-anal plate of *R. uguenoensis* n. sp.

number of callosities and in having the lateral margins blackish. It differs from the above-mentioned species in its general coloration, especially in its bright yellow stripes also encircling the eyes. The hind tibiae of *R. uguenoensis* are bluish, a character also found in *R. nguruense*. However, Jago (1981) described the hind tibiae of *R. nguruense* as bright blue, whereas they are only slightly blue in *R. uguenoensis*. *R. usambaricum* also has bright blue tibiae, but may be easily distinguished by its also having dark blue knees of the hind legs. The different *Rhainopomma* species are mostly restricted to certain mountain massifs, another identification aid.

Jago (1981) mentions that the genitalic system is quite uniform within the genus, so little information can be gained here. In Fig. 4 the apices of the penis of several *Rhainopomma* species are shown. Not much variation exists between these species.



Fig. 4. Apex of penis of *Rhainopomma* species: a. *R. magnificum*, b. *R. montanum*, c. *R. pseudomontanum*, d. *R. uguenoensis*.



Fig. 5. Dorsal aspect of male head of *Altiusambilla keniensis* n. sp. Scale 1 mm.

Remarks.— Individuals collected at lower altitudes were generally much larger than specimens from the montane zone, e.g., from forest clearings. For measurement, individuals were taken from all localities to show variability of size; Means are not useful because size is so strongly a function of elevation. The same phenomenon is observed for *R. magnificum* from the South Pare Mts: Jago (1981) described this species as large; however, specimens from the montane zone are much smaller, resembling in size other *Rhainopomma* species;

Table 3. Comparison of measurements (mm) of *R. magnificum* published by Jago (1981) with data by CH.

R. magnificum	means for males (Jago 1981)	male 1900 m
head width	4.28	2.9
interocular distance	0.31	0.3
posterior femur length	9.28	6.1
posterior femur depth	2.74	1.6
total body length	17.57	10.6

Genetical analyses proved that all individuals collected in a transect from 640 to 1900 m on the South Pare Mts belonged to the same species. The transect was started at the type locality of *R. magnificum*, Gonja forest in the northern foothills of the South Pare Mts, following the road upslope to the village Vuje and further up above the village Chabaru, where disturbed montane forest starts at about 1600 m. Additional material was investigated from Mt. Shengena, 1900 m. The smallest individuals were found in montane forest.

Altiusambilla keniensis Hemp n. sp.

Holotype.— male, Kenya, Mt. Kenya, 1720 m, herbaceous undergrowth of disturbed montane forest, Chogoria route, 3/03, Depository: MNB.

Paratype.— 1 female, same data as holotype, Depository MNB.

Description. - Male: Color: a pattern of black, brown and green. Head and antennae: head and fastigium rugulose; upper part of frons, between antennal bases moderately concave and widened; groove of vertex ending just behind narrowest approximation of compound eyes dorsally, two ridges separating it from the occiput, which is as in A. modicicrus highly pitted (Fig. 5). Antennae uniformly brown or greenish. Thorax: pronotum smoothly rounded and as in A. modicicrus with faint but clearly visible median carina. Well developed dorso-lateral pronotal yellow stripes, ventral cream-yellow band broader. Legs: green with knees of hind femora and tarsi brown. Abdomen: brown with cream dorsolateral stripes continuing for about 2/3 of length of abdomen. Tergites of abdomen carinulate. Posterior margin of ninth abdominal tergite concave, bearing two black tubercles (Fig. 6). Ninth abdominal tergite with median ridge. Supra-anal plate with cone-like elevated black tubercles, especially anterior pair of tubercles elevated. Apex of penis as shown in Fig. 8. Apex of penis larger than in A. modicicrus, reflecting the larger size of the species. Otherwise this structure is typical for the genus Altiusambilla.

Female: Larger and more plump than male (Fig. 18, Pl. IV). Color pattern not as contrasting as in male, but also with conspicuous lateral cream-yellow fascia on pronotum with a less conspicuous fascia dorsolateral on pronotum. As in male, tergites of abdomen carinulate. Dorsal median pronotal carina forming a hump in the



Fig. 6. Supra-anal plate and last abdominal tergites of male *Altiusambilla keniensis* n. sp. Scale 1 mm.



Fig. 7. Dorsal view of female abdominal apex of *Altiusambilla modicicrus* (left) and *A. keniensis* n. sp. (right).



Fig. 8. Male genitalia of *Altiusambilla* species: apex of penis of *A. keniensis* (left) and *A. modicicrus* (right).



Fig. 9. Molecular phylogeny of *Altiusambilla* species based on DNA sequences from the mitochondrial 16S rDNA locus. Bootstrap values (1000 replicates) at nodes in the order: distance, ML, MP.

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Fig. 10. Distribution map of investigated *Rhainopomma* spp. and of *Altiusambilla modicicrus* in East Africa. Map modified from: Karte des Forschungsgebietes der Graf Samuel Telekischen Expedition in Ost-Afrika 1887-88. See also PLATE I.



Legend

- ▲ Altiusambilla
- Rhainopomma
- Usambilla

Fig. 11. Distribution of East African Lentulidae: *Altiusambilla, Rhainopomma* and *Usambilla*. Species screened molecularly (see Schultz *et al.*, 2007) are indicated in black; uninvestigated species are transversely lined symbols.

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metazona. Supra-anal plate broad with ninth tergite modified into groove with median ridge (Fig. 7).

((((((()))))))))		
	males $(n = 1)$	females $(n = 1)$
head width	3.5	4.2
interocular distance	0.4	0.8
pronotum	2.9	4.2
posterior femur length	8.1	10.5
posterior femur depth	2.0	2.5
total body length	13.7	17.5

Measurements (mm).—

Diagnosis.— In *A. modicicrus* there are transverse carinulae in a depressed anterior part of the fastigium, these lacking in *A. keniensis* where this region is rugulose. The transverse fastigial carinulae of *A. modicicrus* are very tiny and proved a character of no generic value being absent in *A. keniensis*.

The anterior part of the fastigium between the antennal sockets is not as wide and concave as in A. modicicrus; both male and female A. keniensis are clearly larger than A. modicicrus (Fig. 19, Pl. IV). The supra-anal plate of A. keniensis bears elevated black tubercles, while in A. modicicrus the tubercles are only slightly raised as in, e.g., other Rhainopomma species. A character found in both Altiusambilla species is a pair of black tubercles at the posterior margin of the ninth abdominal tergite. This character is not known from any other lentulid species and might be a useful generic character. But this must be proven when other Altiusambilla species are found. In both species the tergites of the abdomen are carinulate, a character also absent in Rhainopomma or Usambilla species. In female A. keniensis the supra-anal plate is much broader, while it is elongated in A. modicicrus. Otherwise the supra-anal plates of both species are smooth without tubercles. In A. keniensis the ninth abdominal tergite is medially depressed with a median ridge. In A. modicicrus the ninth abdominal tergite is tiny and unmodified (Fig. 7).

Discussion

The majority of Lentulidae are distributed throughout southern Africa (Schultz *et al.*, 2007). Only five genera have their center of diversity in tropical Africa. Since molecular phylogeny shows, that all three East African genera investigated by Schultz *et al.* (2007) are monophyletic in origin, it can be presumed that only one branch of lentulids reached tropical Africa. Rapid speciation took place when those ancestors became established. The genus *Usambilla*, rich in species, might be the more basic group which gave rise to

Rhainopomma. Rhainopomma species are found on most Eastern Arc mountains (Figs 10, 11, Pl. I), crystalline basaltic mountains of great geological age (about 30 My), and surely more collecting activity will result in more species belonging to this genus. Each mountain massif of the Eastern Arcs apparently harbors "its own" *Rhainopomma* species: there is only one area documented where the ranges of the single *Rhainopomma* species are overlapping [*e.g.*, probably in the area of the eastern side of the South Pare Mts lying adjacent to the West Usambaras (Jago 1981)].

Rhainopomma ancestors probably spread over the whole area of the Eastern Arcs at a time when climatic conditions were different from the present day, where the mountains and thus suitable habitats for *Rhainopomma*, are climatically isolated from each other. This conclusion is prompted by both morphology and molecular data. Morphologically all species are very similar and hard to identify and also genetic distances are rather low. Thus *Rhainopomma* species are

closely related to each other indicating that speciation is geologically young. Stanley and Olson (2005) found similar processes in shrews distributed over the southern branch of the Eastern Arc mountains. They also state that the karyotypic distinction of *Sylvisorex megalura* may represent a relatively recent apomorphy.

Another indicator that a spread of *Rhainopomma* ancestors took place at a time when climatic conditions allowed an exchange of forest taxa is that *Rhainpomma* species of adjacent mountain ranges are the most closely related. Thus *R. montanum* from the Taita Hills in southern Kenya, being geographically further separated from the northern part of the eastern Arcs on the Tanzanian side, is clearly molecularly more distant from the species of the northern part of the Eastern Arcs. These four mountain ranges are situated like a chain from west to south and their faunas are closely related to each other (Fig. 10, Pl. I).

Little can be said about Altiusambilla since only two species are known at present (Figs 9, 19, Pl. IV). This genus seems to be distributed more northwesternly in the highlands of East Africa. Ecologically Altiusambilla has similar requirements to Rhainopomma, inhabiting open forest and forest edges and equivalent habitats. Although the North Pare mountains are very close to Mt. Kilimanjaro (closer together, e.g., than North Pare to South Pare) and both mountain massifs share some montane taxa (e.g., Aerotegmina, Anthracites, Amytta, Chromothericles), Rhainopomma never reached Kilimanjaro and Altiusambilla did not spread into the forests of the Eastern Arcs. It must be presumed that the genera had already differentiated before the geologically young volcanoes Mt. Kilimanjaro or Mt. Meru were built up providing habitat. Dispersal and later speciation of the single Rhainopomma species must have occurred geologically later at a time when the young inland volcanoes were already there. This would explain why certain genera have representatives on almost all mountain massifs, geologically old or young.

Acknowledgments

We gratefully acknowledge grants from the Deutsche Forschungsgemeinschaft and thank the Tanzanian Commission for Science and Technology for permitting research. Appreciation to all members of the molecular lab at the ZFMK and to all colleagues in Bayreuth, Bochum and Bonn. Special thanks to our reviewers Hugh Rowell and Glenn Morris for very useful comments, improving the manuscript considerably.

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Fig. 12. Male *Rhainopomma montanum* (left) from the Taita Hills and *R. pseudo-montanum* n. sp. (right) from the West Usambara Mts. See also PLATE II.



Fig. 13. Male *Rhainopomma pseudomontanum* lateral view (above) and dorsally (right) at forest edge of Mazumbai forest reserve, West Usambara Mts, 1500 m. See also PLATE II.

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Fig. 14. Female R. pseudomontanum, same locality as male of Fig. 13. Lateral view (left) and dorsally (right). See also PLATE III.



Fig. 15. Male *Rhainopomma uguenoensis* n. sp. This species occurs in the North Pare Mts of Tanzania from about 1400 to 2100 m. See also PLATE III.

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Fig. 16. Female *R. uguenoensis* from the Ngofi forest reserve of the North Pare Mts. See also PLATE III.

Fig. 17. Lateral view of male *Altiusambilla keniensis* n. sp. See also PLATE IV.

Fig. 18. Lateral view of female *Altiusambilla keniensis* n. sp. See also PLATE IV.

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Fig. 19. Dorsal view of male *A. modicicrus* (left) and *A. keniensis* n. sp. (right). See also PLATE IV.